WINTER AREAS AND MIGRATORY TACTICS OF NORTHERN GANNETS (MORUS BASSANUS) BREEDING IN NORTH AMERICA

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by

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Abstract

Migration has evolved to allow organisms to undertake life history functions in the most appropriate place at the most appropriate time. Migration creates seasonal ecological linkages that have important implications for survival, population dynamics, response to climate change and species conservation. Yet, knowledge of the wintering areas, migratory routes and timing of migration for individuals and populations are unknown for most avian species, particularly seabirds.

This is the first study to electronically track migration and wintering of gannets breeding in North America. Data from band returns and geolocators were integrated to investigate migratory connectivity and the timing and execution of migration in Northern Gannets (*Morus bassanus*) from four large North American colonies.

Gannets had distinct wintering areas and aggregated into several major hotspots. Most adults remained along the northeast North American coast closest to their colonies and breeding populations displayed weak migratory connectivity. Unexpectedly, the Gulf of Mexico was revealed to be an important wintering area for adults. Gannets displayed remarkable winter site fidelity with extensive range overlap across years.

Timing, rates of movement and use of stopovers during migration depended strongly upon winter destination and also upon sex, colony and year. Females departed the colony prior to males in fall but, contrary to prediction, earlier spring arrival of males was not detected. Variation in the ecological constraints operating during different seasons was emphasized by faster and shorter spring migrations in comparison to fall migrations. The repeatability of migratory duration, distance, and timing of arrival and

departure from the winter grounds suggested strong individual programs for these traits. However, variability in the timing of colony departure and arrival, migratory speed, and the extent of stopovers en route implies greater involvement of environmental inputs into these behaviours.

This is the first study to report two strikingly different migration strategies involving trans-Atlantic migration in a continental-shelf migrant seabird. Three gannets displayed a radically different migration and over-winter strategy by undertaking the first recorded (and repeated), wind-assisted, round-trip trans-Atlantic migrations to the coast of Africa, crossing the Atlantic Ocean in as little as five days. The departure timing and routes of west-to-east (and to a lesser extent east-to-west) oceanic crossings were adjusted to maximise the assistance of winds generated by large weather systems; indicating the use of choice in the execution of this remarkable feat for a normally continental shelf migrant. The discovery of this trans-Atlantic connection has implications for interaction, connectivity and phylogeographic radiations between the eastern and western Atlantic populations.

The observed patterns of migratory timing and scale-dependent connectivity present a novel opportunity to assess the ecological and conservation implications of specific threats during migration and on the wintering grounds. The lability of migratory tactics in the population as a whole combined with remarkable individual consistency in some, but not all, migration parameters offer rare insight into the relative contributions of genetic and environmental factors controlling migration.

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1 Introduction

Organisms undertake different life history functions (e.g. reproduction, non-breeding survival) in the most appropriate place at the most appropriate time in order to maximize fitness (Stearns 1992; Gauthreaux 1982). To support this, migration – defined here as the "seasonal return movement between breeding and wintering grounds" (Newton 2008) – has proven to be a remarkably labile trait. It has evolved across a broad range of taxa many times as an adaptive response to temporal and spatial variation in patterns of resource availability (Griswald et al. 2010; Dingle and Drake 2009; Piersma et al. 2005). It is likely to evolve whenever winter season survival is enhanced away from the breeding grounds and reproduction is more successful outside the winter area (Lack 1954).

Populations may be limited by both biotic and abiotic factors including availability of food and habitat, predation rates, parasite loads and climate change (Both et al. 2006; Cairns 1992; Croxall and Rothery 1991; Lack 1968b) and these can be complicated by interactions with changing climate (Both et al. 2006). Of these, food, both for provisioning young during breeding and for winter survival, is likely the most important ultimate factor limiting migrant bird populations (Lack 1968b). The relative importance of population limiting factors that operate in the breeding versus winter seasons has been widely debated (reviewed in Gauthreaux 1982). But, it is becoming clear that a more holistic viewpoint is required since effects in one season carry over into subsequent ones (Inger et al. 2010; Newton 2008; Norris and Marra 2007; Harris et al. 2005; Norris 2005; Gaston 2003; Marra et al. 1998).

Events during one phase of an animal's annual cycle can carry over into subsequent periods (Marra et al. 1998). Seasonal ecological linkages (Fretwell 1972) in migratory organisms affect individual survival and population dynamics (Sorensen et al. 2009; Norris and Marra 2007; Pütz et al. 2006; Harris et al. 2005), local adaptation and evolutionary response to climate change (Carey 2009; Wilcove and Wikelski 2008; Both et al. 2006), disease epidemiology (Rappole et al. 2000; Olsen et al. 1995) and species conservation (Martin et al. 2007; Webster et al. 2002; Haney et al. 1998). To understand how these linkages affect a species' ecology, evolution and conservation (Boulet and Norris 2006; Webster et al. 2002), it is essential to assess animal spatial distribution and movement throughout the annual cycle.

1.1 Migratory connectivity

The concept of migratory connectivity characterizes the degree to which breeding populations overlap in space and time during the winter (and vice versa) (Webster et al. 2002). Weak (or diffuse) migratory connectivity occurs when separate breeding populations mix freely on the wintering grounds (or vice versa, e.g. Mallory et al. 2008) whereas with strong connectivity a wintering area is spatially partitioned among breeding populations (Webster et al. 2002). These are two extreme ends of a continuous spectrum and most species likely fall somewhere in between. Migratory connectivity provides a powerful theoretical framework to assess population effects (Webster and Marra 2006; Webster et al. 2002). Variable winter conditions can reduce survival in some populations however subsequent effects on population dynamics depend upon the degree of migratory

connectivity between breeding and wintering populations. For example, unusually cold night-time temperatures at a key Mexican Monarch Butterfly (*Danaus plexippus*) wintering site killed an estimated 200 – 300 million animals in just two days during January 2002 (Webster and Marra 2006). Due to strong migratory connectivity, the subsequent effects on population dynamics (and likely changes in density-dependent reproductive success) were only experienced by the eastern North American breeding population which winters in a small number of Mexican sites, compared to western Monarchs that over-winter in California (Hobson et al. 1999).

Migratory connectivity may play a role in local adaptation to wintering grounds. Under strong migratory connectivity, breeding populations (e.g. seabirds from a single colony) mostly migrate to the same wintering area and therefore experience similar selective pressures during both breeding and winter seasons. This may lead to strong local adaptation if birds consistently use the same wintering areas in subsequent years (Webster et al. 2002). Whereas, under weak migratory connectivity, birds from a single breeding population migrate to a variety of winter locations and thus gene flow between these winter populations limits local adaptation (Webster et al. 2002). This, of course, assumes a strong genetic component to migratory behaviour and random mating of birds from different winter populations on the breeding grounds (Gillis et al. 2008; Berthold 1996). On the other hand, weak migratory connectivity will likely permit a more rapid and favourable evolutionary response to shifting selective pressure from climate change and habitat loss or modification, due to genetic variation in migratory behaviour (Norris et al. 2006; Webster and Marra 2006; Dolman and Sutherland 1994). The spread of

parasites and diseases (e.g. Lyme Disease, West Nile Virus, Avian Influenza Virus) among avian populations and subsequently to humans can also be affected by the extent to which breeding and wintering populations overlap (Lebarbenchon et al. 2009; Ricklefs et al. 2006; Webster et al. 2002). For example, the trans-hemispheric spread of Lyme Disease was likely due at least in part to seabirds that migrate between high latitude breeding and wintering areas in different hemispheres (McCoy et al. 2003; Olsen et al. 1995). Effective avian conservation planning depends on knowledge of biogeographical linkages between breeding and wintering populations (Harris et al. 2009; González-Solís et al. 2007; Norris et al. 2006; Lopes et al. 2006) and their relative threats from sources including wind farms (Masden et al. 2009; Fox et al. 2006; Garthe and Hüppop 2004), oil spills and other contaminants (Álvarez and Pajuelo 2004; Wiese and Robertson 2004; Wiese et al. 2001), fishery interactions (Grémillet et al. 2008; Delord et al. 2008; Benjamins et al. 2008; Suryan et al. 2007; Weimerskirch et al. 1997), artificial nocturnal lighting (Montevecchi 2006), changing environmental conditions (Grémillet and Boulinier 2009; Harris et al. 2009; Sandvik et al. 2005) and interactions among these factors (Rolland et al. 2008; Hebert 1998). The implications of migratory connectivity can only be understood with knowledge of the migratory routes and wintering areas of individual animals and by extension, populations (Webster et al. 2002). This knowledge is missing for most bird species.

1.2 Migration and timing

Migration has been characterized in many ways and much of the literature has focused on birds to provide the most cogent examples. It can be facultative where the breeding grounds are survivable in winter or obligate where they are not (Dingle and Drake 2009). Migration is considered to be partial if only some individuals leave the breeding or wintering grounds (Sekercioglu 2010; Dingle and Drake 2009), thereby trading off the risk of remaining in a sub-optimal landscape against the cost of migrating to a better one. Different migration strategies may be undertaken by different (sub-) populations (Lopes et al. 2008; González-Solís et al. 2007; Kren and Zoerb 1997) or by different ages or sexes (González-Solís et al. 2008; Gauthreaux 1982). The latter is classically knows as "differential migration" (Dingle and Drake 2009; Catry et al. 2005). Under this phenomenon, the sexes or age classes undertake migration to separate locations or at separate times in order to gain some advantage (e.g. earlier return to breeding grounds) or avoid competition (Cristol et al. 1999; Ketterson and Nolan 1983).

Migration may be undertaken as a single "undistracted" (sensu Dingle 1996) movement (Gill et al. 2009), as a sequence of moves interspersed with stopovers for refuelling (Egevang et al. 2010; Stutchbury et al. 2009; Guilford et al. 2009; Piersma 2007) or as a continuous "drift" that might better be described as dispersal or ranging (Dingle and Drake 2009). Stopovers may be timed to take advantage of resources that occur at predictable locations and times (Beauchamp 2009; Gillings et al. 2007) or occur irregularly in response to stochastic prey aggregations (Phillips et al. 2008; Croxall et al. 2005). In passerines, shorebirds and waterfowl, staging/stopover areas serve to replenish

fuel supplies during migration (Drent et al. 2007; Catry et al. 2004b; Leu and Thompson 2002; Weber et al. 1999). Conditions at stopover sites may affect timing of onward migration and body condition on arrival on the breeding ground, both of which can affect breeding success and fitness (Drent et al. 2006). A complete migratory cycle may require multiple generations to complete (e.g. Monarch Butterfly; Pyle 1981) or may be repeated many times by individual long-lived organisms (e.g. seabirds; Newton 2008). The breeding, stopover and wintering areas may be fixed (i.e. site fidelity) or labile across multiple cycles (Newton 2008).

Different selective forces shape the spring and fall migrations. In most bird groups, there is a decrease in reproductive success (and ultimately fitness) as the breeding season advances, producing selective pressure for early arrival and laying (Drent et al. 2003; Weber et al. 1999, 1998). Yet, arriving too early can impose severe survival penalties due to harsh environmental conditions and/or limited food supply (Drent et al. 2003; Moller 1994). Birds must therefore time their departure from winter grounds in order to reach the breeding area at the most appropriate time. This is accomplished by an endogenous rhythm that is further fine-tuned by local and global environmental cues including weather and photoperiod (Newton 2008; Forchhammer et al. 2002; Gwinner 1986). Arrival (and breeding) synchrony may play a more important role than absolute arrival date in colonial breeding seabirds (Reed et al. 2009; Hatchwell 1991).

Birds may not be under the same pressure to reach the wintering grounds, and thus migrate more slowly during fall (Newton 2008). The date of fall departure from the breeding site is fairly consistent between years for many species (Newton 2008). But,

spring arrival timing may carry over into fall departure time, since birds arriving late in the spring will generally require the same amount of time to breed as their early arriving conspecifics and thus their fall departure will be delayed (Newton 2008).

The location of the wintering area can affect the timing of migration and subsequent arrival for breeding. In general, spring migration starts earlier in the more distant portions of the winter range, allowing more distant birds to "catch up" (Newton 2008; Bregnballe et al. 2006). Although birds wintering closer may arrive earlier and enjoy greater success (Mehl et al. 2004; Hötker 2002), this is not universal (Bregnballe et al. 2006). Timing of arrival may also be affected by conditions at stopover sites (Drent et al. 2003; Weber et al. 1998). Individuals may need to the reach a specific nutrient threshold for egg production (Perrins 1996) and the extent to which species are income versus capital breeders (Bond and Diamond 2010; Drent and Daan 1980) may dictate resource accumulation needs at stopover sites (Drent et al. 2006). Thus breeding date may be determined by conditions en route, including weather and inter-/intra-specific competition for food, which carry over to the breeding grounds (Drent et al. 2006, 2003).

Large scale climate affects the timing of migration (Vähätalo et al. 2004; Hüppop and Hüppop 2003; Forchhammer et al. 2002) and timing of breeding (Gaston et al. 2009; Frederiksen et al. 2004; Crick 2004; Both and Visser 2001) in birds. For example, changes in climatic conditions have advanced the spring peak in food availability in the Canadian Arctic by 17 days, but Thick-billed Murres (*Uria lomvia*) have advanced their lay date by only 5 days (Gaston et al. 2009). Birds are constrained in how much they can advance their breeding timing by the timing of migration. Since timing of migration is

likely genetically controlled by endogenous rhythms that are not affected by climate change (Gwinner 1986), there is a limit to the extent to which birds can adjust their breeding timing to match prey availability (Both and Visser 2001). In contrast, breeding dates for gannets (Wanless et al. 2008) and other seabirds (Frederiksen et al. 2004) in the eastern Atlantic have been getting later, with no conclusive explanation of why this should be so. The authors of both these studies hypothesized that density dependent differences in intra-specific interference due to growing colonies (Lewis et al. 2001) could be causing gannets to take longer to reach breeding condition. Wanless et al. (2008) also hypothesized that rising sea surface temperatures causing temperature-induced reductions in prey availability through changes in prey abundance, distribution and phenology could be a contributing factor. However, no correlation between timing and either local environmental conditions or large-scale climate (i.e. North Atlantic Oscillation, NAO) was found for either study and the results were inconclusive.

1.3 The role of the sexes

Differential migration is common in many avian species and this pattern is likely the rule rather than the exception, particularly in temperate and polar birds (Catry et al. 2005; Cristol et al. 1999). Males may arrive before females in the spring (Morbey and Ydenberg 2001) and/or depart after females in the fall (Mills 2005; Morbey and Ydenberg 2001). The extent to which the sexes experience different selective pressures and threats during different parts of the annual cycle can have important implications for sex-biased mortality (McFarlane-Tranquila et al. 2010). The differential in relative timing

of migration by males and females is greatest in species with different parental roles. For example, male ducks do not provide parental care and depart the breeding grounds far in advance of females (Newton 2008). The development of avian differential migration research has tended to focus on waterfowl, raptors, shorebirds and passerines (e.g. Mathot et al. 2007; Komar et al. 2005; Carbone and Owen 1995; Arnold 1991). A comprehensive review by Cristol (1999) included only a single seabird species displaying differential migration by the sexes (Great Cormorant, *Phalacrocorax carbo*). More recently, sex-based differences in migration timing, routes and/or destination has been found in several procellariiform seabirds (Phillips et al. 2009, 2005, 2004a; González-Solís et al. 2008; Álvarez and Pajuelo 2004; Weimerskirch and Wilson 2000). Knowledge of the pattern and variation in the winter spatial distribution, and connectivity of individuals, age-classes, sexes and populations of seabirds is a crucial first step in understanding the influences that these factors have on seasonal interactions, population dynamics, life history strategies, evolution of migratory patterns, and habitat and genetic conservation requirements (González-Solís et al. 2007; Norris et al. 2006; Boulet and Norris 2006; Catry et al. 2004a; Webster et al. 2002).

1.4 Site fidelity

Fidelity to breeding and winter sites occurs to a variable extent across species in birds, with some displaying fidelity in both seasons, greater fidelity in one season than the other, or none at all (Newton 2008). For many species, far more is known about breeding season fidelity than winter site fidelity, although the extent of even breeding

season fidelity is unknown for most species. Individuals displaying winter site fidelity may have an advantage over dispersers due to both local knowledge of resources and genetic local adaptation, but dispersing to novel sites may allow individuals to find better habitat (Newton 2008). The extent of winter site fidelity may depend upon demographic parameters (e.g. age or sex), upon the variability of winter habitat and food supply (Newton 2008) and may be influenced by mating systems (Robertson et al. 2000). Winter site fidelity has been shown for waterfowl (Robertson and Cooke 1999), shorebirds (Johnson et al. 2001; Burton 2000), and passerines (Holmes and Sherry 1992; Staicer 1992), but for few seabird species because of the difficulty in observing birds away from the breeding colony. The availability of tracking devices suitable for seabirds is changing this (Wilson et al. 2002) and mixing among (González-Solís et al. 2007) as well as fidelity to (Phillips et al. 2008, 2006; Croxall et al. 2005) non-breeding sites has recently been shown for a small number of mostly southern hemisphere procellariiforms. Yet, the observation of winter site fidelity in Great Cormorants (Frederiksen et al. 2002) may indicate that this behaviour is common across seabirds.

Fidelity to stopover sites, like breeding and wintering sites, varies by taxonomic group (Newton 2008). For most of the few passerines that have been studied, stopover site fidelity was quite low (Catry et al. 2004b; Veiga 1986) although there are exceptions (Merom et al. 2000; Payevski 1971). This is not surprising considering that most passerines migrate across a broad front over vast areas of suitable habitat containing an immense number of likely stopover sites (Newton 2008). Higher fidelity is expected with

species that follow specific narrow migratory pathways, such as raptors and storks, or that have few suitable refuelling sites, such as waterfowl and shorebirds (Newton 2008).

1.5 Seabird migration and over-wintering

Avian ecology has been well studied during the breeding season (Hamer et al. 2002; Lewis et al. 2002; Garthe et al. 2000; Birt et al. 1987; Gaston and Nettleship 1981; Lack 1968a). But, much less is known about survival, feeding ecology, migration and distribution during the non-breeding season. This is particularly true for seabirds and therefore migration and winter ecology have been far better studied in landbirds than in seabirds (Greenberg and Marra 2005).

Assessing migratory connectivity in seabirds has been challenging due to the difficulty in tracking animals throughout the annual cycle (Webster and Marra 2006). Following breeding, many seabird species cross vast oceanic and hemispheric expanses to reach distant shelf-edge, coastal and pelagic wintering areas (Nelson 2002; Harrison 1983). Traditional assessments of migration routes and wintering areas and their associated connectivity have relied on at-sea surveys, band recoveries or even variation in plumage and morphology (Boulet and Norris 2006). Analyses of these data provided an important broad scale picture of occurrence and movements for some species (Bairlein 2003), but limited plumage and morphological differentiation and low band encounter rates have hampered progress, especially for seabirds (Boulet and Norris 2006). Band recoveries are essentially one-off records and do not yield information about the destinations, timing or travel routes of individual migrations. Major insights into seabird

migrations and their spatial and temporal movement tactics over the world's oceans have recently been forthcoming from miniaturized bird-borne tracking and data-logging devices (Ismar et al. 2011; Dias et al. 2010; Yamamoto et al. 2010; Ismar et al. 2010a; Kubetzki et al. 2009; Shaffer et al. 2006; Croxall et al. 2005; Phillips et al. 2004b; Weimerskirch and Wilson 2000), intrinsic biological markers (Phillips et al. 2009; Ramos et al. 2009a; Ramos et al. 2009b; Lopes et al. 2008) and from both techniques used in combination (Phillips et al. 2007). These techniques, especially when integrated with band data can generate a comprehensive understanding of the movement ecology of marine birds over a range of spatial and temporal scales and provide insights into the implications of population connections (Navarro et al. 2009; Strandberg et al. 2009; González-Solís et al. 2007).

Patterns of seabird migration and wintering are highly variable across species but there are general trends within and across taxa. Movement between breeding and wintering areas does not occur on a broad front but instead follows recognizable routes that are defined by oceanographic processes that concentrate prey (Elphick 2007; Yoder et al. 1994). Adult round-trip migration typically occurs over smaller spatial and temporal scales than that of juveniles (Newton 2008; Nelson 2002). Migratory movements vary from short (or not at all in some partial or non-migrants) to long-distance whole-ocean movements. For example, North American cormorants undertake a partial migration that is largely restricted to coastlines (Nelson 2005). At the other end of the spectrum, many procellariiforms migrate across open ocean in association with oceanic fronts and stable wind patterns (Shaffer et al. 2006; Weimerskirch and Wilson 2000) and Arctic Terns

(*Sterna paradisaea*) complete annual trips in excess of 70,000 km by migrating along coastal shelves and across open ocean (Egevang et al. 2010).

Spring arrival at the breeding colony (and subsequent laying) is highly synchronized in many seabird species (e.g. Reed et al. 2009; Hatchwell 1991) which may require birds wintering at more distant locations to initiate migration earlier in order to arrive on time (Bregnballe et al. 2006). The consistency of migration timing across years has received little attention in seabirds, although consistent timing has been found in Black-browed Albatross (*Thalassarche melanophrys*; Phillips et al. 2005) and Cory's Shearwater (*Calonectris diomedea*; Dias et al. 2010). Use of stopover areas, or "hotspots", a common feature of migration in other orders (Stutchbury et al. 2009; Beauchamp 2009), has recently been observed in some seabirds (Dias et al. 2010; Egevang et al. 2010; Guilford et al. 2009; Phillips et al. 2005) but not others (Yamamoto et al. 2010; Shaffer et al. 2006). Finally, individual animals may display markedly different migratory patterns (Dias et al. 2010; Kubetzki et al. 2009) that aggregate into population level migratory strategies.

A variety of methods have been developed to study bird migration and wintering (Gauthreaux 1996). Prior to the 1990s, most knowledge about bird migration resulted from either visual observation or banding studies. Visual observation can provide good information on timing of movement at breeding sites or along routes, and the location of over-winter areas at the species or population level. But, the lack of information on provenance or the ability to follow individual birds severely limits the inferences that can be drawn. Banding studies elucidate provenance and have provided invaluable

information that is limited by hidden biases introduced by unequal spatial and temporal recapture probability. This is particularly problematic for seabirds that winter at sea. Recoveries are typically from dead birds that wash up on coastlines (perhaps far from where they died) and recovery rates are strongly correlated with coastal human population density and distribution. Radar monitoring has provided important information on landbird migration (Bonter et al. 2009) but has seen use for seabirds in only a small number of studies (Masden et al. 2009; Gudmundsson et al. 2002). This technology shows promise, especially with the proliferation of coastal weather radar sites (Gasteren et al. 2008), but it too suffers from issues of provenance and even species identification. Recent developments in electronic technology are revolutionizing the study of bird migration allowing the year-round tracking of individual animals (Burger and Shaffer 2008; Wilson et al. 2002). These bird-borne devices are being applied to an ever-growing list of species as cost, package size and power requirements decrease (e.g. Stutchbury et al. 2009). Natural patterns of chemical isotope gradients are proving to be a cost-effective way to link breeding and wintering areas at a large spatial scale (Phillips et al. 2009) but again individual routes and strategies remain elusive.

Each of these techniques carries with it attendant biases, cost/benefit tradeoffs and constraints on the spatiotemporal scales and types of inferences that can be drawn. The most successful studies are likely to be those that combine two or more of these approaches (Strandberg et al. 2009; Phillips et al. 2007; Furness et al. 2006). But, few authors have explicitly compared inferences drawn from multiple methods for a given

species (but see Strandberg et al. 2009; Anker-Nilssen and Aarvak 2009; Harris et al. 2009).

1.6 Study species

The Northern Gannet (*Morus bassanus;* hereafter gannet) is the largest seabird breeding in the North Atlantic (Nelson 2002) and is the focus of this study. It and its two congeners, the Cape Gannet (*M. capensis*) and the Australasian Gannet (*M. serrator*), along with the boobies (6 species), make up the family Sulidae (Nelson 1978). The Sulidae is in the order Pelicaniformes that includes the pelicans (Pelecanidae), cormorants and shags (Phalacrocoracidae), anhinga and darter (Anhingidae), frigatebirds (Fregatidae) and tropicbirds (Phaethontidae; Nelson 2005). The three gannets are the only migratory high latitude sulids, relying on cool productive waters for breeding. The rest of the family are essentially non-migratory tropical residents (Nelson 2005).

Cape Gannets breed at six main colonies in South Africa and Namibia and number *ca.* 173,000 breeding pairs. Colonies in Namibia have suffered sharp declines since the 1950s possibly in relation to interaction with fisheries (Okes et al. 2009; Crawford 2007; Nelson 2002). Non-breeders occur along both the east and west coasts of Africa, with juveniles moving further (most between 2,000 and 4,000 km) than adults (mostly < 500 km, but up to 3,380 km; Nelson 2005). The world population of Australasian Gannets (> 70,000 pairs) breeds around New Zealand (mostly the North Island) and to a lesser extent in southeastern Australia and Tasmania (Figure 1; Nelson 2005). Juveniles disperse up to 5,000 km along the east and south coasts of Australia

(Ismar et al. 2010a) before returning to breed after several years at sea. Most adults are reported to remain in New Zealand coastal waters during the non-breeding season (Nelson 2005) but some have recently been tracked to coastal Australia (Ismar et al. 2011).

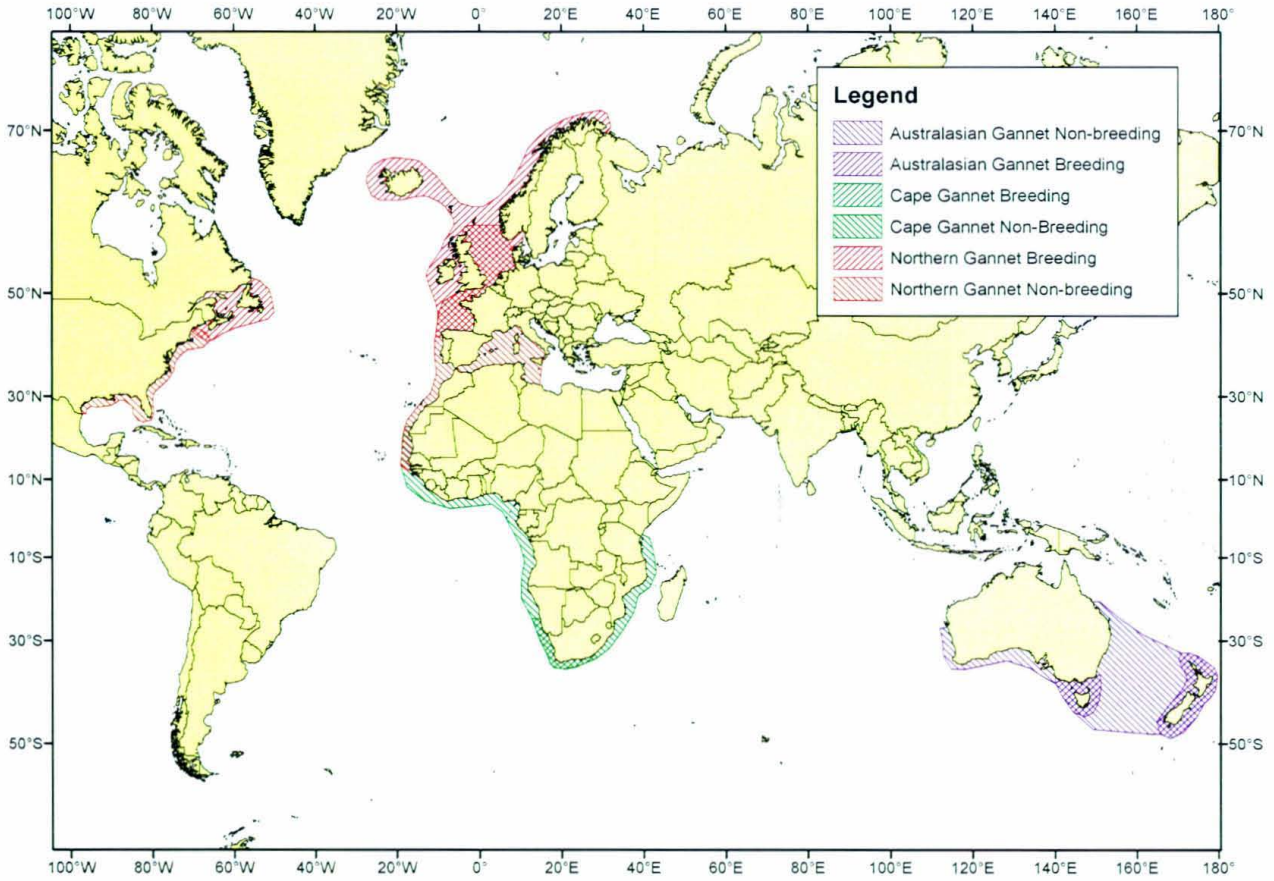

Figure 1. World ranges of Northern Gannet (*Morus bassanus*), Cape Gannet (*Morus capensis*) and Australasian Gannet (*Morus serrator*). Sources (Kubetzki et al. 2009; Nelson 2005, 2002)

The Northern Gannet breeds at 45 colonies in the North Atlantic; 31 in Europe (from France to Norway), 8 in Iceland and 6 in North America (Nelson 2005). The world population (measured in apparently occupied sites (AOS) at colonies) totals *ca.* 421, 000 AOS (304,000 in the Eastern Atlantic and 117,000 in the Northwest Atlantic; Nelson 2005; J. Chardine, pers. comm.). From banding studies and observations of birds at sea, Nelson (2002) ascertained that juvenile gannets fledged in the UK migrate down the west coast of Europe, into the Mediterranean, as far south as the highly productive waters off Senegal and Mauritania in the Canary Current where extensive fisheries produce large amounts of discards (Camphuysen and van der Meer 2005). Nelson (2002) deduced however, that most adults remain closer to the breeding colony in the North Sea, in the Bay of Biscay and along the Iberian coast.

Recently, Kubetzki et al. (2009) used geolocator tracking to reveal that adult gannets breeding at Bass Rock, Scotland occupied relatively small home ranges within one of four distinct geographic zones in proportions that differed from expectation. Surprisingly, almost half wintered off western Africa indicating the existence of weak to moderate connectivity in this population (Kubetzki et al. 2009). This represents a likely change in migratory strategy or, alternatively, the effect of bias in previous banding studies. Currently, there is no evidence of colony-based differences in winter destination for European gannets, although most studies have focused on only the colony at Bass Rock (Nelson 2002). Repeated tracking of individuals was recommended to interrogate the extent of consistency within individual schedules across years (Kubetzki et al. 2009). It might be expected that male gannets would winter closer to the colony than females

(Ketterson and Nolan 1983). This activity could confer an advantage to males that could return to the colony earlier by shorter routes, in order to defend nest sites early in the season (Nelson 2005). Large scale differences in winter locations have not been found between the sexes, but there was a tendency for Bass Rock females to winter further from the colony than males (Kubetzki et al. 2009) and gannets displayed sex differences in foraging behaviour during the breeding season in some (Lewis et al. 2001) but not other (Garthe et al. 2007b) cases.

There was little variation in the timing of spring return to the colony for Bass Rock gannets that wintered in four distinct wintering areas separated by several thousand kilometres (Kubetzki et al. 2009) implying that more distant birds either begin their migration earlier or migrated faster than those wintering closer to the colony. Geolocator-tracked adult gannets departed Bass Rock over a ~3 week period with a median date that varied slightly between years and there was great individual variation in the timing and routes of migratory movements (Kubetzki et al. 2009). Several gannets had stopovers in the North Sea or Norwegian Sea before continuing on to their winter grounds. Spring migration was initiated over a fairly narrow time window (end of January to mid-February) and the duration of fall and spring migrations were similar (Kubetzki et al. 2009).

Far less is known about the migration and wintering of gannets breeding in North America. Current knowledge of their migration is due to at-sea surveys and long-term banding studies, conducted mainly at two of the gannets' six North American breeding colonies (Bonaventure Island and Funk Island; Gaston et al. 2008). They migrate from

eastern Canadian breeding colonies along the continental margin to wintering areas along the U.S. east coast and Gulf of Mexico, covering up to *ca.* 5,000 km one way at speeds of 24 – 32 km d^{-1} (Gaston et al. 2008; Nelson 2005). The main target locations for wintering were considered to be off the east coast of Florida and in the Gulf of Mexico based on the large number of (mostly immature) recoveries in these areas (Gaston et al. 2008; Nelson 2002). At-sea surveys in Canadian waters indicate that gannets were observed south and east of Newfoundland and on the Scotian Shelf during November/December (Fifield et al. 2009; Brown 1986). Gannets were present over the continental shelf from the Gulf of Maine to Chesapeake Bay during December – February, with the highest densities (and survey effort) occurring between New Jersey and Cape Cod (Powers 1983). Juveniles and immatures reportedly migrate further than adults, supported by the fact that only 8 % of adult band recoveries were in the Gulf of Mexico (Nelson 2002). Spring migration begins as early as February and birds arrive at the breeding area in mid-April having covered the return distance more quickly than in fall at a speed of 56 – 112 km d^{-1} (Gaston et al. 2008; Nelson 2005) via a route that may be further offshore and than in fall (Perkins 1979). Many of these band recoveries are decades old and the extent to which inferred winter areas have remained constant over time is unknown, as is their reliance on band recovery biases.

Band returns indicate a lack of colony-based differences (i.e. weak connectivity) in North American winter location, although the number of such returns is small and the degree to which band recovery biases affect this conclusion is unknown. Winter and breeding season segregation of populations has been found in other seabirds (Ramos et al.

2009b; Rayner et al. 2008; González-Solís et al. 2007; Weimerskirch and Wilson 2000) and is expected in wintering gannets, particularly those breeding in different oceanographic regimes (e.g. Bonaventure Island in temperate waters and Funk Island in sub-Arctic waters; Garthe et al. 2007b). The extent to which gannets breeding in North America exhibit differential distance migration remains unknown.

Gannets are birds of continental shelf waters (Nelson 2002). The Atlantic Ocean likely acts as a rarely-crossed barrier to interactions between Nearctic and Palearctic populations. Only nine gannets banded in North America have been reported in the eastern Atlantic (Gaston et al. 2008). Most of these were immature birds in their first year of life and presumed to be lost. The risk and energy demand associated with trans-Atlantic movements underscore the evolutionary forces that shape migratory behaviour, with important ramifications for population interactions and species range radiations (Berthold 2001; Able 1999; Alerstam 1981). Questions of trans-Atlantic population interactions, historical range expansions, and ancestral source population remain unresolved for gannets.

1.7 Thesis objectives and structure

The goal of this thesis is to examine the migratory movements and winter areas of adult Northern Gannets breeding in North America. This research addresses three important questions: (1) what degree of migratory connectivity and overlap in winter area exists in the population as a whole, between colonies and between sexes (i.e. where do they go?), (2) how and when is the migration accomplished with respect to timing of

movements and stopovers by different populations and sexes (i.e. how and when do they get there?) and (3) how consistent are these patterns for individuals across years? These questions are addressed in the context of a comparison and integration of signals derived from band recoveries and electronic tracking of individual birds. Different levels of ecological organization (population, colonies, sexes and individuals) are compared in all sections.

Sections 3.1 and 4.1 focus on the migratory connectivity and pattern of space use of North American breeding gannets. Gannets are anticipated to remain within North American continental shelf waters throughout the year. Data from bands and geolocators are integrated to investigate winter locations and patterns of connectivity in breeding adult North American gannets. Overall and inter-colony patterns of wintering areas and space use are compared, as are those of the sexes. Since prey are not likely evenly distributed, but instead aggregated to form a patchy distribution, gannets are predicted to exhibit weak to moderate overall connectivity by targeting specific destinations within their North American winter range (Kubetzki et al. 2009). Based on banding data, the Florida coast and areas further north along the southeastern and mid-Atlantic states are likely be prime wintering areas. Birds from separate colonies likely overlap to some extent, but based on observations of other species and a lack of conclusive evidence to the contrary in gannets, colony-based segregation is predicted. Males are expected to winter nearer their colonies than females, allowing shorter return to nesting sites prior to females (Nelson 2005). Winter site fidelity is being increasingly reported in seabird tracking studies (Dias et al. 2010; Phillips et al. 2006, 2005; Croxall et al. 2005;

Weimerskirch and Wilson 2000) and has been observed in the gannet's sister family, the cormorants. Given the benefits that accrue from knowledge of local prey distribution, it is likely that gannets too will display some degree of similarity in choice of wintering area across years.

Sections 3.2 and 4.2 investigate the more dynamic elements of the migration itself addressing the timing and speed of migration and the use of stopover sites en route to the wintering grounds. Like many colonial birds, gannets breed synchronously which likely constrains the variability in colony arrival date. Colony departure date is constrained by chick growth which depends upon a variety of factors including individual parental quality and experience. Variation in these factors will likely lead to greater variability in adult fall departure date in comparison to spring arrival date. Extensive individual variation in timing is, however, expected (Kubetzki et al. 2009). There is growing evidence that seabirds make use of specific stopover sites (Dias et al. 2010; Egevang et al. 2010; Guilford et al. 2009; Croxall et al. 2005; Phillips et al. 2005). Gannets have a costly mode of flight requiring high-energy output (Birt-Friesen et al. 1989) that likely must be replenished en route perhaps by halting the migration for stopovers. Most species investigated to date migrate across vast expanses of relatively unproductive ocean environment and have stopovers at specific productive sites. Gannets likely remain over relatively more productive continental shelf/edge waters, where the use of distinct sites may be less pronounced. Colony arrival in spring is likely to be relatively synchronous (Nelson 2002) and if there is significant variation in the distance to individual wintering areas, then distant birds will likely migrate more quickly or depart earlier in order to

achieve this. Males are expected to arrive before females in spring in order to establish their breeding territories (Kubetzki et al. 2009; Nelson 2005). There will likely be variation in timing between colonies due to local variation in the timing of prey availability and weather suitability for breeding and similar variation may be expected between years. If individual gannets winter in similar areas between years, then they are predicted to exhibit similar duration and speed of migratory movements, but local conditions at the breeding colony will likely be a more important determinant of departure and arrival timing than individual consistency (Frederiksen et al. 2004). Finally, spring gannet migrations are predicted to be faster than in fall due to evidence from banding studies (Gaston et al. 2008) and theoretical predictions (McNamara et al. 1998).

Sections 3.3 and 4.3 examine trans-Atlantic migration in more detail. Incidences and proportions of trans-Atlantic crossing are contrasted for gannets breeding in the western and eastern North Atlantic Ocean and in different North American colonies. The effect of wind patterns on the timing of departure for gannets breeding in North America are revealed, as are interactions with populations breeding in the eastern Atlantic.

Section 4.4 considers the ecological, evolutionary and conservation implications of the findings from the foregoing sections, followed by conclusions in section 5.

2 Methods

2.1 Study sites

Research was conducted at four of the six Northern Gannet colonies in the northwest Atlantic (Figure 2): 1) the species' largest colony (~59,600 pairs) at Bonaventure Island (48°29' N, 64°09' W) in the Gulf of St. Lawrence (Québec, Canada), 2) the third largest North American (~14,800 pairs) and the species' southernmost colony at Cape St. Mary's (46°49' N, 54°49' W; Newfoundland, Canada), 3) the fourth largest (~10,000 pairs) and most oceanic North American colony on Funk Island (49°45' N, 53°11' W) off the northeast Newfoundland coast and 4) the fifth largest (~2,300 pairs) colony at Baccalieu Island (48°07' N, 52°47' W) on the eastern Newfoundland coast (Chardine 2000; Chardine unpubl. data).

2.2 Winter zones

The gannet's North American winter range (Nelson 2002) was partitioned into three oceanographic zones for analysis. The boundaries of these zones (Figure 3) were selected on the basis of characteristic thermal regimes and current systems that typify each region and influence prey species assemblages (Rabalais and Boesch 1987). Additionally, each zone has its own unique set of industrial activities (e.g. fishing, petroleum extraction) that could affect wintering gannet populations (Rattner and McGowan 2007). The zones are 1) northeast (NE) – including all the east coast of North America north of Cape Hatteras, 2) southeast (SE) – from Cape Hatteras to the tip of Florida (east of 81° W), and 3) Gulf of Mexico (west of 81° W; GoMex). In the northeast

zone, the continental shelf is strongly influenced by cold Labrador Current water that flows south along the Labrador and Newfoundland coasts (Rabalais and Boesch 1987). In the southeast zone, the warm northward-flowing water of the Gulf Stream dominates the continental shelf until Cape Hatteras where it deflects sharply to the northeast. The clockwise-circulating Loop Current, and the eddies it generates, and outflow from the Mississippi River delta typify the warm Gulf of Mexico (Rabalais and Boesch 1987).

2.3 Data sources and processing

2.3.1 Bands

The North American bird-banding database provided records of all gannet banding and recovery records as of 17 Jan 2006, including 13,494 deployments and 832 known-location encounters. Birds were characterized as "adult" (n = 315) if they were in at least their 5th year of life when encountered, "immature" (n = 469) if they were younger or "unknown" (n = 48). Encounters were filtered to extract only those found during the non-breeding (15 Oct – 15 April; n = 288) and winter (Jan – Feb, and those coded simply as "winter", n = 62). The non-breeding season was defined to coincide with typical gannet colony departure and arrival dates. Winter was restricted to Jan – Feb to allow for comparison with geolocator-tracked birds that had ceased large-scale migratory movements by then (see section 2.3.2). Encounters were classified as "domestic" if birds were encountered on the same continent on which they were banded and "trans-Atlantic" if they crossed the Atlantic Ocean.

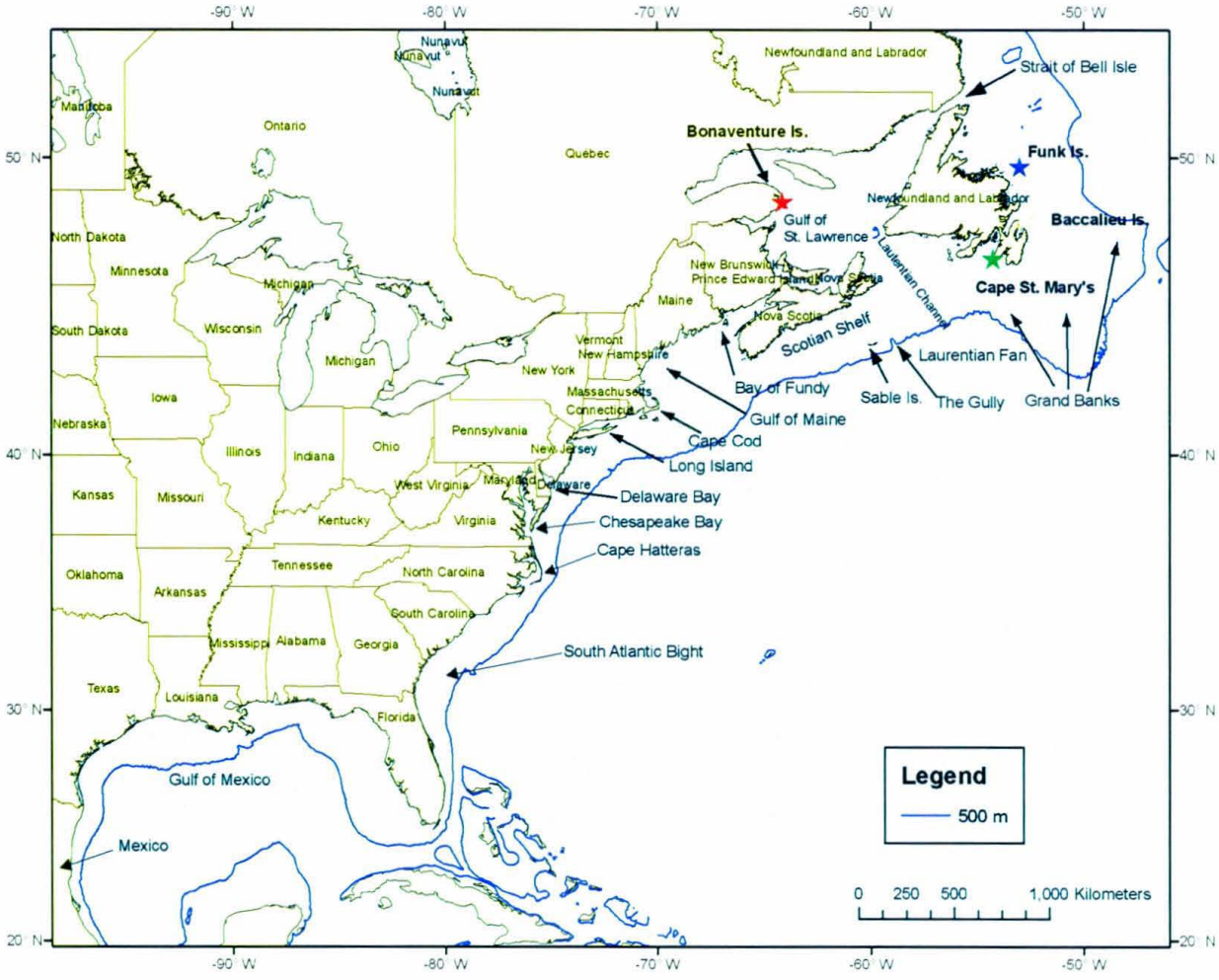

Figure 2. Study area showing colony locations and places mentioned in the text.

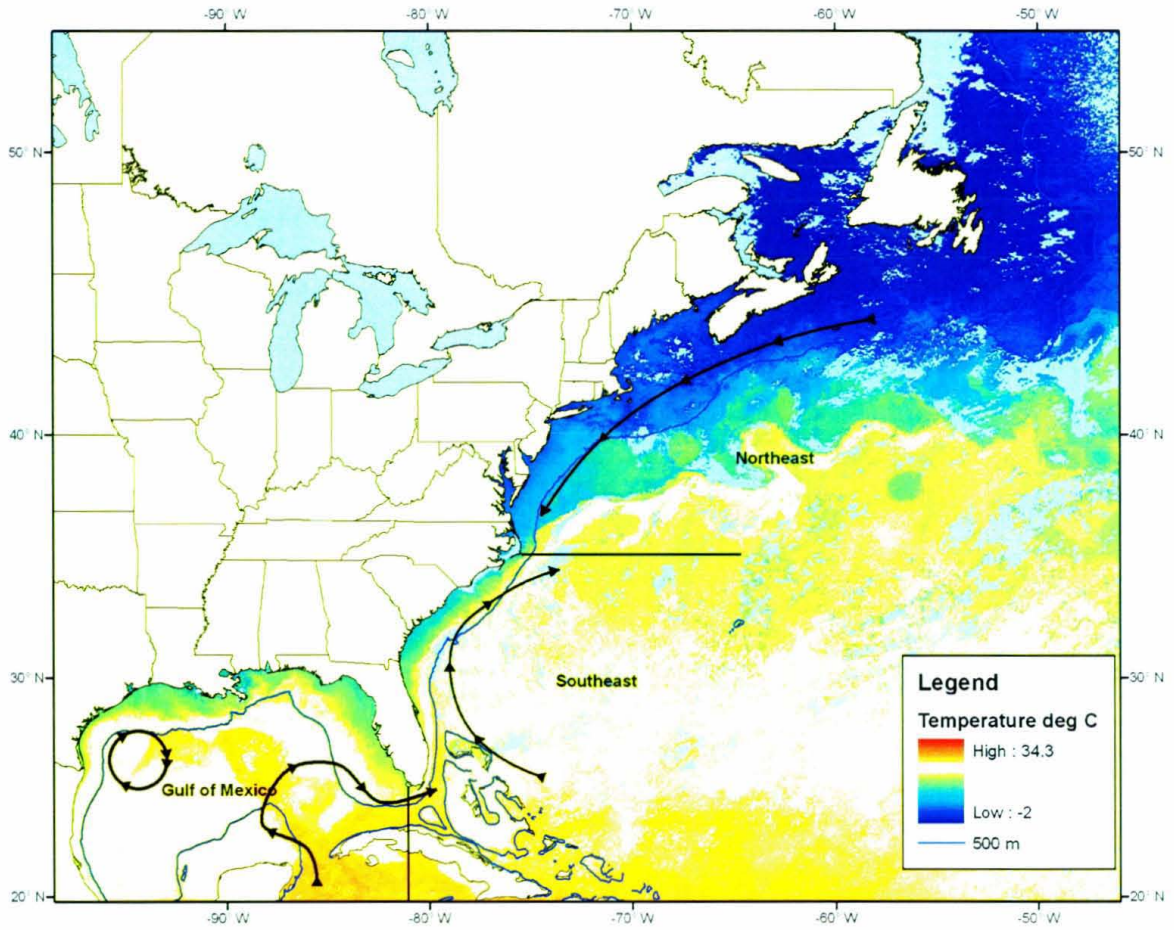

Figure 3. Location of North American over-winter zones, predominant currents, and typical mid-February sea surface temperatures that characterize continental shelf waters.

2.3.2 Geolocators

Three models of light sensing geolocators were used: Geo-LT (cylindrical, 14 x 45 mm, weight: 8.5 g in air, 16.2 g including attachment, Earth & Oceans Technologies, Kiel, Germany), LTD 2400 (cylindrical, 11 x 32 mm, weight: 8 g in air, 8.8 g including attachment, Lotek Wireless, St. John's, NL, Canada) and BAS MK5 (square, 18 x 18 x 5 mm, weight: 3.6 g total, British Antarctic Survey, Cambridge, UK). Geo-LT geolocators recorded light level every 30 s and temperature every 120 s. The LTD 2400 sampled light every 60 s, and temperature and pressure every 32 s. BAS loggers sampled light every 30 s and recorded the maximum level every 10 minutes.

Deployments. Prior to the non-breeding seasons of 2004-05, 2005-06, 2006-07, 2007-08 and 2009-10 a total (across all years) of 50 Earth & Oceans Geo-LTs, 10 Lotek 2400 LTDs, and 6 BAS MK5 geolocators were deployed once or twice (in successive years) on 76 gannets (31 Bonaventure Island, 15 Funk Island, 14 Cape St. Mary's, 16 Baccalieu Island) for a total of 105 deployments (Table 1). Breeding adults with large chicks were captured from nest sites toward the end of the nesting season with a 5 m telescoping noose pole. Birds were held for *ca.* 5 min while devices and identification bands were attached; geolocators were retrieved during subsequent breeding seasons. Gannets were captured from colony peripheries to reduce disturbance, but individuals from the third or fourth row from the edge were selected to avoid a bias toward young or inexperienced breeders that nest at the colony edge (Nelson 2002). All animals were cared for in accordance with guidelines of the Canadian Council on Animal Care.

Bonaventure Island. On 11 September 2004, 25 birds were fitted with devices, and all were recaptured between 24 May and 14 July 2005 (except one recaptured on 3 July 2007; Table 1). One bird lost its device and 4 devices failed, yielding 20 datasets. On 4 – 8 September 2005, 23 birds (17 of the same birds from the previous year and six others) were equipped, and all were recaptured between 12 June and 13 July 2006. Three birds lost devices, yielding 20 datasets.

Funk Island. 14 birds were fitted with geolocators during 5 – 10 August 2005, and 10 were recaptured during 8 – 14 August 2006, 9 of which yielded datasets (Table 1). Eleven gannets (10 of the same birds from the previous year) were equipped 8 – 15 August 2006 and 8 of these were recaptured 24 – 25 July 2007 or 26 – 29 July 2008, yielding 7 datasets.

Cape St. Mary's. On 3 September 2005, a single geolocator was deployed, and was retrieved on 15 September 2006 (Table 1). Five gannets were equipped on 15 September 2006 and one was retrieved on 4 September 2007. Seven gannets were equipped on 16 September 2007 and 4 were retrieved between 10 August and 22 September 2008. On 31 August 2008, 2 gannets were equipped (one same bird from previous year) and one was recaptured on 4 July 2009. This bird was re-equipped on the same day and not recaptured in 2010. From the 7 devices retrieved at this site, 4 datasets were recovered.

Baccalieu Island. Between 15 and 20 August 2009, 16 birds were equipped, 1 was retrieved on 14 April 2010 from a fishing net on the eastern Newfoundland coast and 4

were retrieved as well as one with a broken empty casing during 17 – 25 August 2010, yielding 5 datasets.

Thus, 65 (full or partial) datasets were collected from 46 separate individuals each tracked in 1 or 2 years. Seventeen birds were tracked (with complete round-tip datasets) in two consecutive years. Including both North American and African migrants, all 65 datasets included positions up to the end of December, and 95 %, 92 %, and 89 % (n = 62, 60 and 58) till the end of January, February and March respectively; 86 % (n = 56) yielded complete round-trips. Different numbers of devices/birds are included in each analysis depending on device failure date; sample sizes are given with the description of each analysis.

Table 1. Overall and yearly numbers of Northern Gannets (*Morus bassanus*) equipped, recaptured and datasets recovered at each study colony.

Overall							Yearly Details			
					Datasets recovered					
Colony	Unique birds equipped	Unique birds recaptured	Unique birds providing data[1]	Birds tracked twice[2]	All	Full[3]	Year	Deployments	Recaps.	Datasets recovered
Bonaventure Island	31	31	28	11	40	34	2004-05	25	25	20
							2005-06	23	23	20
Funk Island	15	10	9	7	16	14	2005-06	14	10	9
							2006-07	11	8	7
Cape St. Mary's	14	7	4	0	4	3	2005-06	1	1	1
							2006-07	5	1	1
							2007-08	7	4	2
							2008-09	2	1	0
							2009-10	1	0	0
Baccalieu Island	16	6	5	0	5	5	2009-10	16	6	5
Total	76	54	46	18	65	56		105	79	65

[1] Includes birds providing partial datasets.
[2] Only includes birds with two complete round-trip tracks.
[3] Datasets containing complete round-trip tracks.

Geolocator data analysis. Raw light data from Geo-LT and BAS geolocators were analyzed using MultiTrace for Windows (Jensen Software Systems) which produced two daily position estimates. Longitude is estimated by comparing the time of local noon (or midnight) to Greenwich Mean Time (GMT) while latitude is estimated from day length (Hill 1994; Wilson et al. 1992). For LTD 2400s, internal tag software computed a single daily position based on measured light parameters. The error in the light-based latitude can be more than twice the corresponding longitude error estimated by geolocators (Shaffer et al. 2005; Teo et al. 2004; Phillips et al. 2004b). Light-based latitude cannot be estimated during the solar equinoxes, when day length is the same at all latitudes (Hill 1994). However, light-based latitude estimates can be improved (or recovered during equinoxes) by reconciling geolocator-measured sea surface temperatures (SSTs) with remotely sensed satellite SSTs. Teo et al. (2004) described an algorithm that uses the geolocator longitude estimates and finds the most plausible latitude for each day based on three indices of match between geolocator and remotely sensed SSTs near that longitude. This method was originally developed for bluefin tuna (*Thunnus thynnus*) and subsequently validated for seabirds, reducing overall mean great circle error from 400 km to 202 km (Shaffer et al. 2005). The software developed by Teo et al. (2004) was not available for use in this study, so the algorithm was implemented in Matlab (The Mathworks Inc.) according to their published description, and used to adjust gannet daily latitude estimates accordingly. SST corrected positions were filtered to remove positions requiring unreasonable speeds (n = 31), using a forward-backward averaging filter (McConnell et al. 1992) with a maximum speed of 84 km h^{-1} (Garthe et

al. 2007a). Missing positions (e.g. due to failure of light-based geolocation during equinoxes and/or failure of the SST correction algorithm; n = 1,714, 7.5 %), were linearly interpolated between surrounding positions (Guilford et al. 2009). Tracks of individual birds were smoothed using a sliding window boxcar smoother (with a window size of 5) whereby the coordinates of each smoothed position were the weighted mean (in a 1:2:3:2:1 ratio) of the 2nd previous, previous, current, subsequent and 2nd subsequent position's coordinates. This resulted in a total of 22,871 filtered and smoothed positions. Smoothed positions were characterized as either "travel" or "stopover" based on an examination of inter-position displacements and turning angles. Travel is characterized by relatively small turning angles and displacements exceeding a minimum threshold, whereas stopovers are characterized by relatively large turning angles or small displacements (Turchin 1988). Travel and stopovers were assessed using a sliding window of five consecutive positions, with each bird initially defined to be in the stopover state (i.e. starting at the colony). Transition to the travel state was defined when any three or more positions (within a block of five) had turning angles $\leq 35^{o}$ and inter-position distances $\geq$ 40 km. Likewise, transition from travel to stopover was defined when three or more positions failed to meet the turning angle or displacement criteria.

The masses of eight geolocator-equipped adults taken before deployment and after retrieval in 2005-06 served as an indicator of potential device effects. Additionally, survival and fecundity rates were compared with published accounts (Mowbray 2002).

2.4 Statistical analysis

The geolocator data were notably unbalanced across colonies and years complicating statistical analysis. The bulk of the data came from Bonaventure Island and Funk Island from 2004 – 2006, but Bonaventure Island was the only colony sampled in 2004-05, Cape St. Mary's and Baccalieu Island had small sample sizes and Baccalieu Island was the only colony sampled in 2009-10 (see section 3.1.2). Including all data across all years in statistical models made it impossible to distinguish year effects from colony effects. The data were therefore partitioned for testing of colony and year effects in all tests described below. For colony effects, comparisons were made between Bonaventure and Funk Islands in 2005-06 only, since this was the only year with a sufficient sample at more than one colony. Year comparisons were made between Bonaventure Island in 2004-05 versus 2005-06, and between Funk Island in 2005-06 versus 2006-07. The data for sexes and winter destination were better balanced, with a good spread across colonies and years and models investigating the effect of these parameters used all available data. For all analyses, except those involving linear mixed effects models (LMMs; Pinheiro and Bates 2000), statistical significance was set at a critical $\alpha = 0.05$. P-values from LMMs are know to be approximate (Zuur et al. 2009) so for these models $p \leq 0.01$ was considered significant, $0.01 < p \leq 0.05$ was considered "weak" evidence and $0.05 < p \leq 0.1$ as "marginal" evidence. The following subsections provide details of specific analyses. For all boxplots, the thick horizontal line shows the median, the box edges depict the first and third quartiles, the dashed lines extend to 1.5 times the inter-quartile range and outliers are plotted as individual open circles.

2.4.1 North American wintering areas

Gannet wintering areas were assessed using both bands and geolocators. The number of bands recovered in each oceanographic zone during non-breeding and winter seasons was examined, and the hypothesis of equal zonal usage across colonies of origin was tested. For geolocators, the winter centroid was determined for each gannet whose device functioned until at least the end of February (n = 56 datasets from 40 birds) by calculating the mean latitude and longitude of all positions between the end of fall migration and the start of spring migration (see section 2.4.4). Proportions of birds with centroids in each oceanographic zone were compared among years, and colonies. Since all birds tracked more than once had centroids in the same winter zone across years (except one), data were combined across years (excluding the one bird) to test the effect of sex on the proportion wintering in each zone. Likewise, the proportion of birds wintering in each North American oceanographic zone was compared between bands and geolocators. Trans-Atlantic crossing by gannets from North American and European colonies was investigated using bands and geolocators and the number and ages of birds displaying this behaviour were compared between colonies and continents. All comparisons described in this section were conducted with Fisher exact tests.

2.4.2 Winter space usage

To investigate areas of high use during the entire non-breeding season (including both migration and over-wintering), the Spatial Analyst Density tool in ArcGIS 9.3 (ESRI, Redlands, CA) was used to create a map showing the pattern and locations of hotspots (areas of intense usage) for all birds combined. More in-depth analysis

employed volume-contoured kernel utilization distributions (UDs; Worton 1989; Silverman 1986; van Winkle 1975) for two purposes: 1) to set the boundary of the wintering area in order to define the end of fall migration and the start of spring migration (see section 2.4.4) and 2) to give estimates of space use while in the wintering area. These were constructed from fixed bivariate normal kernels with a grid size of 10 km with the *adehabitat* package (Calenge 2006) in R 2.11.0 (R Development Core Team 2010). The 50 % volume contour defined the winter "core range" and the 95 % contour defined the "home range". These values are commonly used in other seabird studies and in ecology in general (Dias et al. 2010; Laver and Kelly 2008; Wood et al. 2000). Examination of bird positions revealed that most birds had stopped large scale movements and reached the furthest extent of their migrations by January after which they remained in relatively restricted areas with mostly stopover days until at least the end of February. Thus January – February stopovers were used to compute the core and home range kernels. Non-stopover positions were excluded since an examination of migration track indicated some birds had obviously not reached their winter destination by 1 January or had started their spring migration before the end of February. Including these positions would have included (in some cases large) areas that were used for migration and not for over-wintering and thus would have biased both the boundary defining migration timing and winter space use.

The choice of the kernel smoothing bandwidth, h, has the greatest impact on resulting UDs (Silverman 1986). This parameter affects the relative contribution of surrounding points at a given distance to the kernel density estimate at any given point

(Gitzen et al. 2006). Use of the least squares cross validation (LSCV) method of choosing h has been suggested to produce the most accurate results (Seaman et al. 1999; Worton 1995). But, the LSCV algorithm may fail to converge for datasets where many positions are tightly-clumped or co-incident (Gitzen et al. 2006; Hemson et al. 2005); indeed the algorithm failed to converge for many gannet datasets (n = 12). Additionally, LSCV can potentially produce a different smoothing bandwidth for each bird, resulting in UDs with variable levels of detail across individuals. This makes it difficult to decide if any resulting variation between individuals is due to animal behaviour or choice of smoothing parameter (Pellerin et al. 2008). Other authors have used an ad-hoc value, h_{ref}, which is based on the latitudinal and longitudinal variances of the positions (Worton 1989). This approach can also produce a different smoothing parameter for each bird and may overestimate area use (by over smoothing) for animals with multimodal distributions (Gitzen and Millspaugh 2003; Seaman et al. 1999). A constant value of h is thus preferred to clarify comparisons between individuals, colonies and sexes (Tolon et al. 2009; Pellerin et al. 2008; Sternalski et al. 2008), and a value of 75 km was chosen for all analyses, based on the mean h_{ref} (73.5 km, n = 56) for all winter datasets.

The sizes of North American core and home ranges were tested for differences between colonies, years, destination zones, and sexes. LMMs with bird identity as a random effect were used to account for the fact that some birds were tracked more than once. The likelihood of concurrent shared space use for a mated pair from Bonaventure Island tracked during 2005-06 was assessed using the utilization distribution overlap index (UDOI; Fieberg and Kochanny 2005). The UDOI measures the amount of overlap

between UDs, relative to two individuals using the same space in a uniform manner. A UDOI of 1 indicates 100% overlap between two individuals using space uniformly, values < 1 indicate less overlap relative to uniform space use and values > 1 indicate greater overlap relative to uniform space use (Fieberg and Kochanny 2005).

2.4.3 Winter site fidelity

Winter site fidelity was assessed in three ways for birds tracked in two consecutive years. First, regional-scale fidelity was assessed by comparing the zonal location (northeast, southeast or Gulf of Mexico) of centroids in successive years. Second, the distribution of distances between successive winter centroids was compared to the distribution of distances between centroids of datasets paired at random (n = 10,000 randomizations; Dias et al. 2010) with a Kolmogorov-Smirnov test; the medians were also compared for both distributions. This approach can detect a shift in the location of the winter centroid, but is insensitive to changes in range size. To address this, a third analysis compared the percentage overlap between consecutive core and home ranges. For each individual, two indices were computed for each of the core (home) ranges: $CR_{1,2}$ ($HR_{1,2}$), the percentage of the core range (home range) in year one overlapped by the core range (home range) in year two, and $CR_{2,1}$ ($HR_{2,1}$), the percentage of core range (home range) in year two overlapped by the core range (home range) in year one (Fieberg and Kochanny 2005; Kernohan et al. 2001). The significance of these overlap indices was assessed by comparing them to the distribution of overlap indices of core and home ranges paired at random (n = 10,000 randomizations; Dias et al. 2010). The observed and

randomized distributions of overlaps were subsequently compared with a Kolmogorov-Smirnov test and the medians were compared for both distributions.

2.4.4 Migration timing and movement

Fall migration duration was defined as the period from colony departure until first entry into the 95 % winter home range, and spring duration as the period from final exit of the 95 % winter home range until colony return. Geolocator temperature data indicated date of colony departure and return. High and variable night-time temperatures indicated colony attendance and constant low night-time temperatures were characteristic of time spent at sea (Shaffer et al. 2005). Migration speed (in km d^{-1}) was defined as the total distance covered along the migration track divided by the migration duration. LMMs were used to test the effect of colony, year, winter destination and sex on migration start/end date, distance, duration, speed, and number of stopover days for both fall and spring migrations. LMMs were also used compare the same parameters during fall versus spring migrations. Means ± SD and ranges for migration timing parameters are presented in tabular form throughout the results in order to provide a clear summary of these data. Estimated effect sizes from LMMs, which may differ slightly from raw means, are presented in the text. One individual, gannet 14932 breeding at Cape St. Mary's, had no chick, departed prematurely and was thus removed from the departure date analysis.

Consistency of these parameters through time for birds tracked more than once was tested using repeatability statistics (Lessells and Boag 1987). Repeatability is the portion of variation in behaviour attributable to differences between individuals (as opposed to within individuals) in the population as a whole and may (Falconer 1981) set

an upper limit on heritability (but see Dohm 2002). Repeatability, also known as the intra-class correlation coefficient (Sokal and Rohlf 1981), is calculated as $r = s^2_A/(s^2 + s^2_A)$, where s^2_A is the among-individual variance and s^2 is the within-individual variance (Lessells and Boag 1987). A large value of r indicates consistent behaviour since most of the variation is between individuals and not within individuals.

3 Results

Device effects. All (31) equipped birds were recaptured at Bonaventure Island (in both years) as were 10 of 15 birds at Funk Island (the two colonies where the most recapture effort was concentrated). Birds carrying 46 of 48 deployments at Bonaventure Island and Funk Island were seen in the colony the following year, as were 10 of 14 at Cape St. Mary's, and all but one recaptured gannets had an egg or chick. Two equipped gannets seen in the colony, but not recaptured, had lost an egg or chick. Mean body masses did not differ before and after carrying loggers over winter (paired t-test, t = -0.24, df = 7, p = 0.82).

3.1 North American wintering areas

Unless specifically otherwise stated, this section is restricted to a consideration of banded and geolocator-equipped birds that over-wintered in North America. Section 3.3 addresses trans-Atlantic migration.

3.1.1 Bands

In North America, 13,494 gannets have been banded. Of these, up to 2006, only 85 non-breeding season and 20 winter adult recoveries have occurred in North America

(Table 2). The mostly coastal recoveries occurred over a large geographic range from the breeding grounds in the north to the southern tip of Florida and into the Gulf of Mexico as far west as Texas (Table 2; Figure 4). Recoveries did not occur in equal proportions among the oceanographic zones during the non-breeding season. Instead, 59 % occurred in the northeast zone, 35 % in the southeast zone compared with only 6 % in the Gulf of Mexico. This pattern of zonal proportions did not differ when recoveries where restricted to the winter period (Table 2, Fisher exact test, $p = 0.77$).

3.1.1.1 Colony comparison

Only Bonaventure Island and Funk Island had enough recoveries for comparison. There were more than three times as many birds banded at Bonaventure Island (and more recoveries) than at Funk Island, but there was little temporal overlap in recoveries of adults outside the breeding season between the two colonies: Bonaventure Island recoveries occurred from 1939 to 1989 whereas those from Funk Island ranged from 1982 to 1998. This difference reflects the more recent banding effort on Funk Island compared to Bonaventure Island. Recoveries of Bonaventure Island adults during the non-breeding season produced 60 % in the northeast, 34 % in the southeast compared to only 6 % in the Gulf of Mexico (Table 2).

A similar pattern emerged for Funk Island where 46 % occurred in each of the northeast and southeast zones, compared to only 8 % in the Gulf of Mexico. The single recovery from Baccalieu Island occurred in the northeast zone. When colonies were compared, no difference in zonal proportions of recoveries was found for either the non-

breeding (Fisher exact test, $p = 0.68$) or winter (Fisher exact test, $p = 1.0$) periods. Only a single known-sex recovery occurred: a female from Funk Island in the southeast zone.

Table 2. Numbers (proportion) of adult Northern Gannets (*Morus bassanus*) banded and recovered in North America during non-breeding (15 Oct – 15 Apr) and winter (Jan – Feb) in three winter zones: northeast (NE), southeast (SE) and Gulf of Mexico (GoMex).

Banding location	Number banded	Recoveries							
		Non-breeding				Winter			
		NE	SE	GoMex	Total	NE	SE	GoMex	Total
Bonaventure Is.	10,465	43 (0.60)	24 (0.34)	4 (0.06)	71	8 (0.50)	7 (0.44)	1 (0.06)	16
Funk Is.	2,853	6 (0.46)	6 (0.46)	1 (0.08)	13	1 (0.33)	2 (0.67)	-	3
Baccalieu Is.	27	1 (1.0)	-	-	1	1 (1.0)	-	-	1
Cape St. Mary's	42	-	-	-	-	-	-	-	-
Other[1]	107	-	-	-	-	-	-	-	-
Total	13,494	50 (0.59)	30 (0.35)	5 (0.06)	85	10 (0.50)	9 (0.45)	1 (0.05)	20

[1]Gannets banded along the east coast of North American, colony of origin unknown.

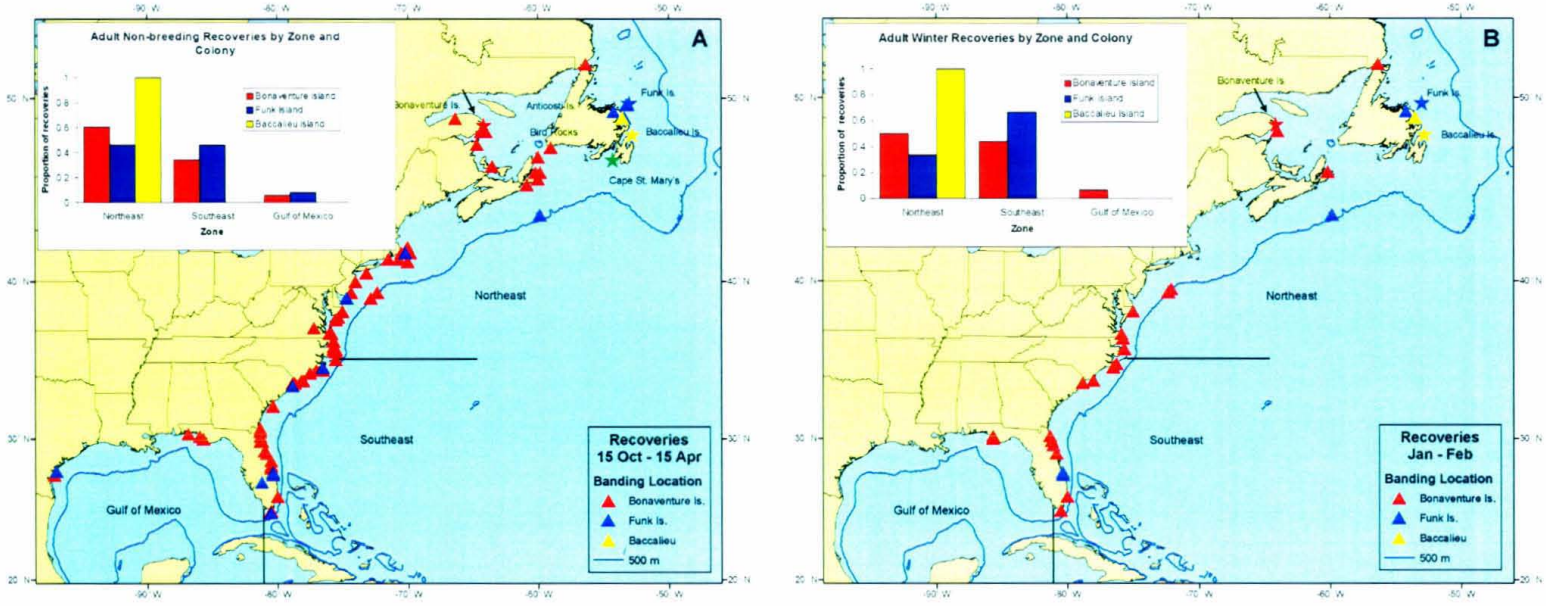

Figure 4. Colony proportion of (A) non-breeding season (15 Oct – 15 Apr) and (B) winter (Jan – Feb) band recoveries of adult Northern Gannets (*Morus bassanus*) in each oceanographic zone.

3.1.2 Geolocators

Geolocators yielded the first round-trip migration records for North American gannets (Figure 5). Forty birds provided 56 migration datasets to end of February in at least one year (Table 3). Three further birds provided partial tracks bringing the North American wintering total to 43 of 46 birds tracked. The remaining three wintered in Africa (see section 3.3). As predicted, gannets mainly occupied continental shelf/slope waters during the non-breeding season, but they were not randomly distributed throughout their winter range (Figure 6). Instead, they aggregated at several primary hotspots: off the coast of New Jersey and around Chesapeake Bay in the northeast zone, and along the Louisiana coast in the Gulf of Mexico. Secondary areas of aggregation also occurred in the Gulf of Maine and in the South Atlantic Bight.

Table 3. Location of winter (Jan – Feb) centroids for 46 geolocator-equipped Northern Gannets (*Morus bassanus*) tracked to locations in North America or Africa.

			Location of winter centroid[1]				
Colony	Bird ID	Sex	2004-05	2005-06	2006-07	2007-08	2009-10
Bonaventure Is.	23937	M	NE				
	23939	M		GoMex			
	23940	F		SE			
	23941	M	SE	SE			
	23942	?	GoMex				
	23943	M	GoMex	SE			
	23944	M	NE	NE			
	23945	F	NE	NE			
	23946	M	NE	NE			
	23947	M		NE			
	23948	M	GoMex	GoMex			
	23949	F	NE				
	23950	F	N. Am.				
	23951	M	N. Am.	NE			
	23952	F	SE	SE			
	23953	?	GoMex				
	23954	M	NE	NE			
	23955	M	NE	NE			
	23956	M	NE	NE			
	23957	?	N. Am.				
	23958	?		GoMex			
	23959	M		NE			
	23961	F		GoMex			
	23963	?		NE			
	76485	M	NE				
	76493	F	NE				
	76495	M	NE	NE			
	13092	M		SE			
Cape St. Mary's	14932	?				GoMex	
	14945	?			N. Am.		
	80164	F				NE	
	80182	?		Africa			
Funk Is.	80172	M		NE	NE		
	80173	F		NE	NE		
	80174	F		GoMex			
	80175	M		GoMex			

			Location of winter centroid[1]				
Colony	Bird ID	Sex	2004-05	2005-06	2006-07	2007-08	2009-10
	80179	M		NE	NE		
	80180	F		NE	NE		
	80181	M		GoMex	GoMex		
	80183	M		N. Am.	NE		
	80185	F		Africa	Africa		
Baccalieu Is.	16206	?					NE
	16207	?					GoMex
	16208	?					NE
	16295	?					Africa
	16210	?					NE
Column Totals			20	30	8	2	5

[1] NE = northeast, SE = southeast, GoMex = Gulf of Mexico, N. Am. = in North America – centroid location unknown due to premature device failure.

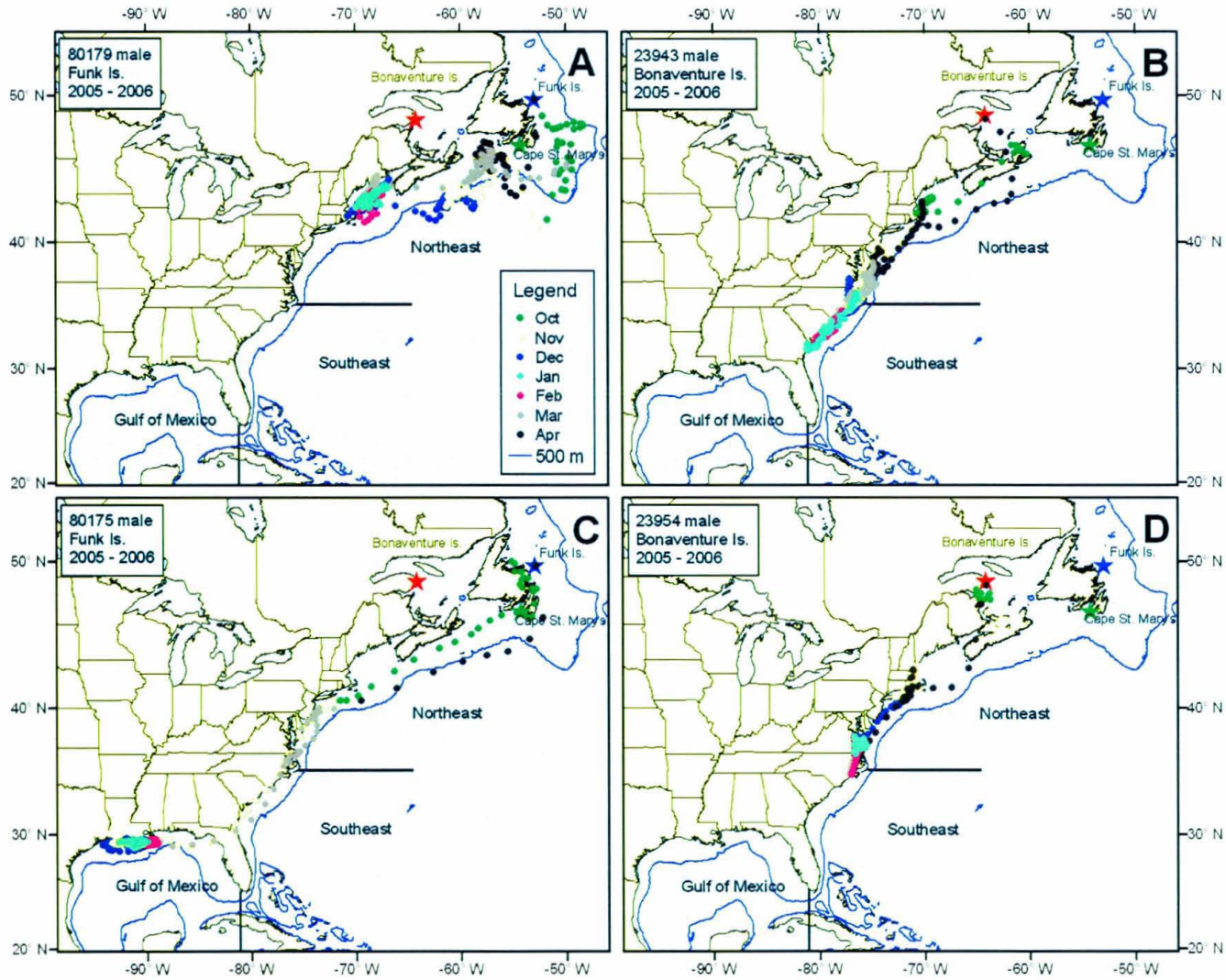
A
80179 male
Funk Is.
2005 - 2006
B
23943 male
Bonaventure Is.
2005 - 2006
C
80175 male
Funk Is.
2005 - 2006
D
23954 male
Bonaventure Is.
2005 - 2006
Bonaventure Is.
Funk Is.
Cape St. Mary's
Northeast
Southeast
Gulf of Mexico
Legend
Oct
Nov
Dec
Jan
Feb
Mar
Apr
500 m
-90° W
-80° W
-70° W
-60° W
-50° W
50° N
40° N
30° N
20° N

Figure 5. At-sea positions of four individual geolocator-equipped Northern Gannets (*Morus bassanus*) showing typical patterns of wintering (Jan – Feb) in the three North American oceanographic zones: (A) northeast, (B) southeast, (C) Gulf of Mexico and (D) northeast. Jan – Feb positions were restricted to the Gulf of Maine, Carolinas, Gulf of Mexico and Chesapeake Bay areas respectively. Dots represent bird positions (two per day).

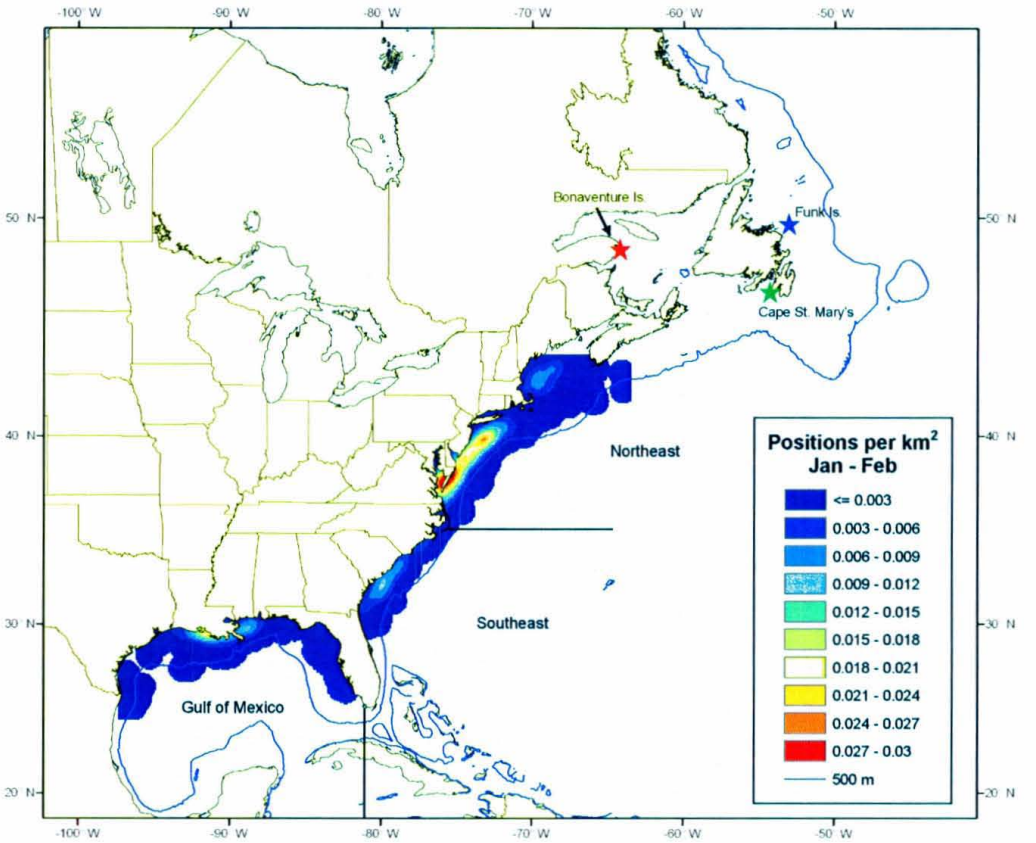

Figure 6. Density of twice-daily positions from geolocator-equipped Northern Gannets (*Morus bassanus*) during Jan-Feb (all birds combined) showing location of primary hotspots in the northeast and Gulf of Mexico zones and the secondary hotspots in the Gulf of Maine and South Atlantic Bight.

3.1.2.1 *Winter centroids*

Of the 40 birds that provided 56 North American datasets complete to the end of February, the location of the winter centroid varied among individuals (Figure 7). Many birds wintered in the northeast zone, occupying shelf waters from the Gulf of Maine to

Cape Hatteras. Others had centroids in the southeast zone, along the coasts of North Carolina, South Carolina, Georgia and northern Florida. Still others occupied the shelf waters of the Gulf of Mexico from Florida to Texas. Gannets did not use each of the three zones in equal proportions. The percentages of North American wintering gannets (n = 39; excluding one bird that used different zones in different winters) using each zone were 62 % in the northeast zone, only 10 % in the southeast, and 28 % in the Gulf of Mexico (Table 4). Three further birds had partial tracks but still provided useful information. At the date of failure (6 Jan – 3 Feb), these birds were all still in North American waters and presumably stayed there, since no bird wintering in Africa departed at such a late date. One of these birds (gannet 23950) had reached and spent its last 10 days before device failure in the Gulf of Mexico, the other two (gannets 23957 and 14945), failed in the northeast zone. Including all birds is important when estimating the proportion of the North American breeding population potentially exposed to the aftermath of the *Deepwater Horizon* oil spill in the Gulf of Mexico (Montevecchi et al. 2011). The percentage of adults that entered the Gulf in at least one year was 28 % (n = 13 of 46; Table 4).

There was variation in the wintering area within each zone. For example, within the northeast zone, some birds remained in the northern portion of the zone, almost entirely within the Gulf of Maine (Figure 6, Figure 7). Others congregated in the southern part of the zone around Delaware and Chesapeake Bays. Birds in the southeast zone tended to frequent the coasts of North Carolina, South Carolina, Georgia and northern Florida, avoiding the rest of the Atlantic Florida coast. Most birds in the Gulf of Mexico

inhabited coastal Louisiana waters but two gannets restricted themselves to the extreme east of the Gulf and a third to the extreme west.

The shortest (great-circle route) distance between the breeding colony and the winter centroid across all years was 1,041 km and the longest was 3,947 km. Mean (± SD) distances for each year were similar: 2004-05: 1,851 ± 752 (n = 17), 2005-06: 2,098 ± 846 (n = 27), 2006-07: 2,091 ± 949 (n = 6), and 2007-08: 2,808 ± 1,379 (n = 2), and 2009-10: 2,348 ± 672 (n = 4).

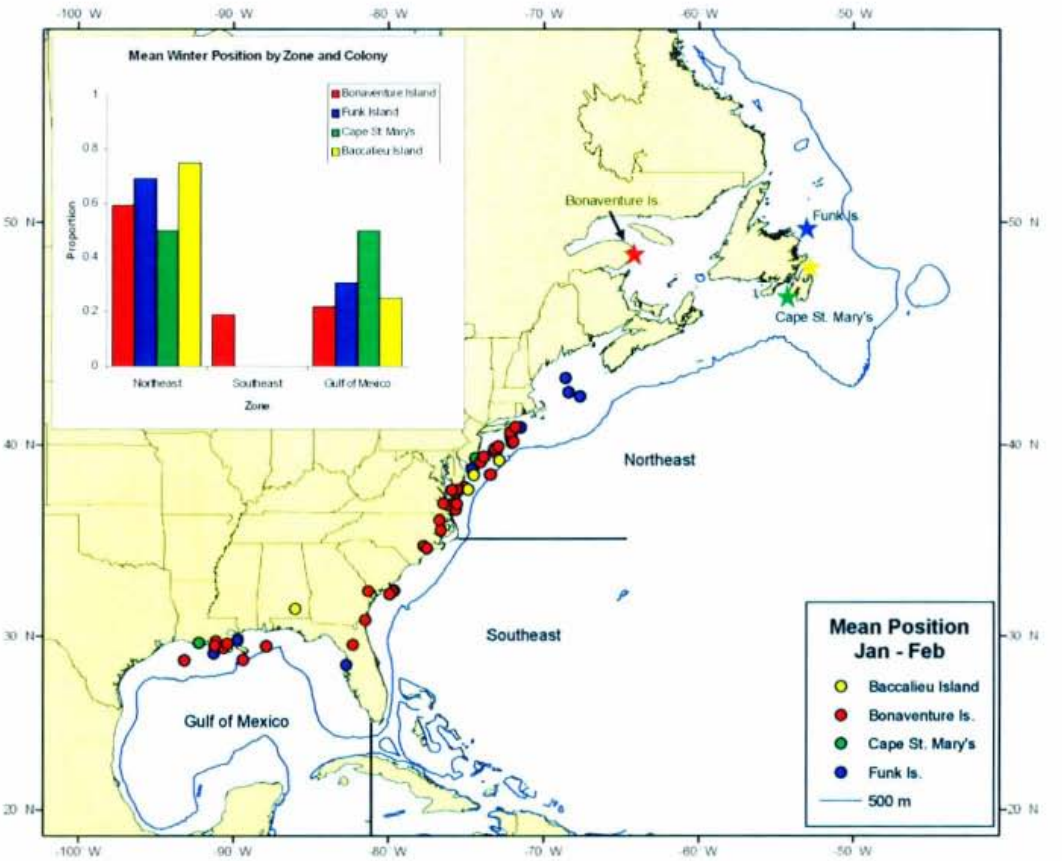

Figure 7. Location of winter (Jan – Feb) centroids from 56 datasets of 40 adult geolocator-equipped Northern Gannets (*Morus bassanus*) tracked in 1 or 2 years between 2004 and 2010, according to oceanographic zone and colony. One Baccalieu Island centroid is on land in Alabama due to an early January stopover in the southeast zone followed by wintering along the Louisiana coast.

Table 4. Numbers (proportion) of geolocator-equipped Northern Gannets (*Morus bassanus*) with complete winter (Jan – Feb) dataset centroids in each of the North American oceanographic zones by year, colony and sex. Birds tracked across multiple years are included only once in combined and total rows.

	Northeast	Southeast	Gulf of Mexico	Total
Year:				
2004-05	11 (0.65)	2 (0.12)	4 (0.23)	17
2005-06	15 (0.56)	5 (0.18)	7 (0.26)	27
2006-07	5 (0.83)	0	1 (0.17)	6
2007-08	1 (0.50)	0	1 (0.50)	2
2009-10	3 (0.75)	0	1 (0.25)	4
Colony:				
Bonaventure Island				
2004-05	11 (0.65)	2 (0.12)	4 (0.23)	17
2005-06	11 (0.55)	5 (0.25)	4 (0.20)	20
Combined[1]	15 (0.60)	4 (0.16)	6 (0.24)	25
Funk Island				
2005-06	4 (0.57)	0	3 (0.43)	7
2006-07	5 (0.83)	0	1 (0.17)	6
Combined	5 (0.62)	0	3 (0.38)	8
Cape St. Mary's				
2007-08	1 (0.50)	0	1 (0.50)	2
Baccalieu Island				
2009-10	3 (0.75)	0	1 (0.25)	4
Sex:				
Male[1]	14 (0.70)	2 (0.10)	4 (0.20)	20
Female	6 (0.60)	2 (0.20)	2 (0.20)	10
Grand Totals[1]	24 (0.62)	4 (0.10)	11 (0.28)	39

[1] Excludes one male bird that was in the Gulf of Mexico in 2004-05 and the southeast in 2005-06.

Inter-year comparison. In 2004-05 and 2005-06, most North American wintering gannets had centroids in the northeast zone, with fewer in the Gulf of Mexico and fewest in the southeast zone (Table 4). During 2006-07, 2007-08 and 2009-10 tracked gannets only had centroids in the northeast (the majority) and in the Gulf of Mexico. Bonaventure Island and Funk Island were the only colonies with enough data to compare across years. The proportion in each zone was not statistically significant at Bonaventure Island between 2004-05 and 2005-06 (Fisher exact test, $p = 0.66$) or at Funk Island between 2005-06 and 2006-07 (Fisher exact test, $p = 0.56$).

Colony comparison. More birds from Bonaventure Island had winter centroids in the northeast zone than in either of the other two zones in both 2004-05 and 2005-06 (Figure 7; Table 4). Over both years combined, 60 % of Bonaventure Island birds had winter centroids in the northeast zone, which was more than double that in any other area. Bonaventure Island birds were the only ones with centroids in the southeast zone during any year. Birds from Funk Island had centroids in only the northeast (62 %) and Gulf of Mexico (38 %). Three of the four Baccalieu Island birds wintered in the northeast while the fourth was in the Gulf of Mexico. Of the two Cape St. Mary's birds, one was in the northeast and the other was in the Gulf of Mexico. When colonies were compared (Bonaventure Island versus Funk Island in 2005-06), there was no significant difference in proportional usage of each zone (Fisher exact test, $p = 0.34$).

There was a difference in the pattern of how winter centroids of birds from different colonies were distributed within the northeast zone (Figure 5, Figure 7). Birds from Funk Island tended to have a more northerly distribution, with two birds hardly

venturing further south than the Gulf of Maine during the entire winter (e.g. Figure 5A). Centroids of birds from Bonaventure Island were concentrated in the southern half of the zone, particularly around Delaware and Chesapeake Bays, as where those from Baccalieu Island (although Baccalieu Island birds were tracked in a different year than all others). Further, no Newfoundland gannet had any positions south of Cape Hatteras, unless it was in transit to or from the Gulf of Mexico.

Sex comparison. Across all years, 31 known-sex gannets (21 male, 10 female) were tracked to winter areas within North America. Contrary to prediction, both sexes were found throughout the species' winter range (Figure 8; Table 2, Table 4) and there was no evidence that males wintered closer to the breeding colony than females. The proportion with centroids in each oceanographic zone did not differ between the sexes (excluding gannet 23943 that switched from the Gulf of Mexico to the southeast between years; Fisher exact test, $p = 0.85$). This result did not differ if 23943 was included in the Gulf of Mexico or southeast sample (Fisher exact test, both $p \leq 0.73$). One mated pair (male: 23951, female: 23952) was tracked from Bonaventure Island in 2005-06 during which the male's winter centroid was in Chesapeake Bay in the northeast zone and the female's was *ca.* 600 km away off the coast of South Carolina in the southeast zone (Table 4).

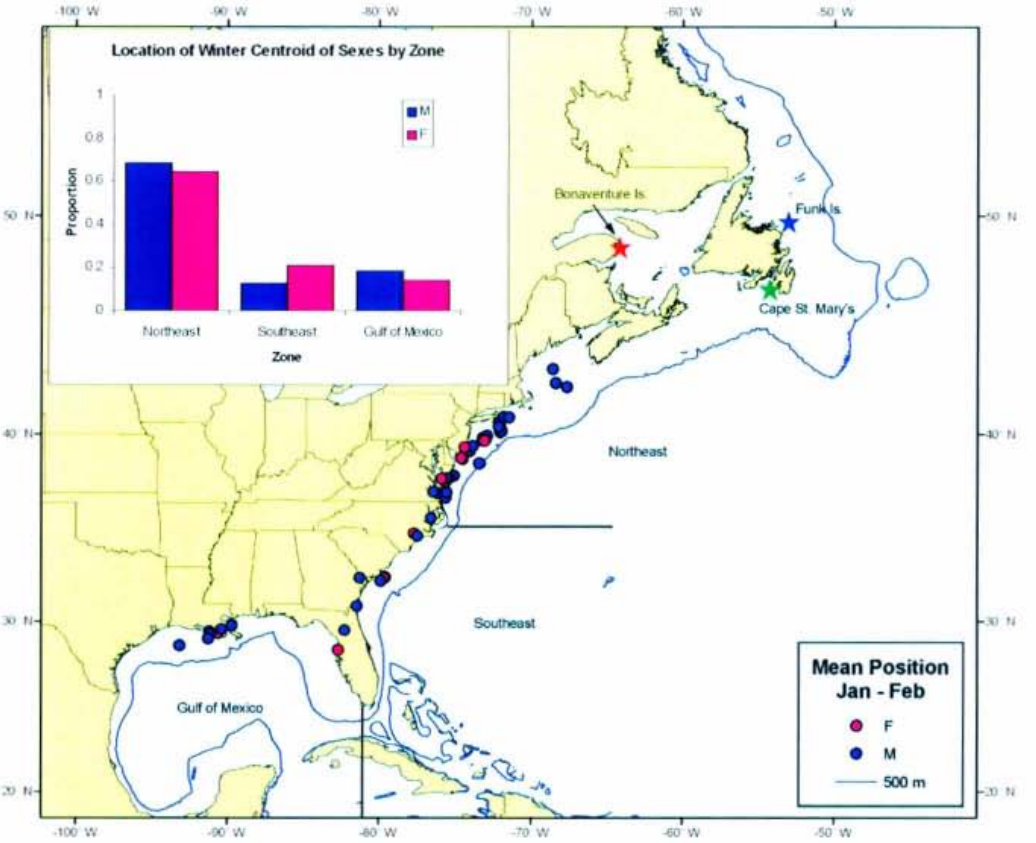

Figure 8. Location of winter (Jan – Feb) centroids of 47 datasets from 31 adult known-sex geolocator-equipped Northern Gannets (*Morus bassanus*) tracked in 1 or 2 years according to sex and oceanographic zone. Stars indicate locations of colonies.

3.1.2.2 Space use

Examination of home and core ranges provided more insight into individual variation than winter centroids. Most birds spent the winter period in relatively small areas and did not range widely (Figure 9; Figure 10), although there was significant individual variation. Home and core range sizes ranged from 153,600 to 606,300 km^2 and 34,600 to 137,100 km^2, respectively. Mean ± SD home range size, 273,605 ± 87,211 km^2 was equal to the area of a circle with a radius of only 292 ± 45 km (range: 221 to 439 km), while mean core range size, 58,877 ± 19,246 km^2 was equal to that of a circle with a radius of only 135 ± 21 km (range: 105 to 209 km). Some birds (n = 8) with centroids in the northeast and southeast zones had a small portion of their home range that crossed the northeast-southeast dividing line in one or more years. Three further birds with centroids in the northeast made considerable excursions into the southeast (e.g. Figure 10D). The most extensive of these, gannet 23954, remained entirely in the northeast zone in 2004-05 with core and home ranges centered in Chesapeake Bay and in the Gulf of Maine. But in 2005-06, its home range covered almost all the area from the northern Gulf of Maine to the coast of Georgia. In this year, its core range consisted of three similar sized disjoint areas, one in the Gulf of Maine, one in Chesapeake Bay, and one in the South Atlantic Bight. Of these 11 birds whose ranges crossed the northeast-southeast boundary, all were from Bonaventure Island, and the male/female ratio (7 males, 3 females) did not differ from the sex ratio for known sex birds in the study (Fisher exact test, p = 1.0). Another gannet (gannet 16207) bird stopped in the southeast sector for the first two weeks of January and then moved to the Gulf of Mexico for the rest of the winter. Its home range

was partially in the southeast and partially in the Gulf of Mexico but its core range was entirely in the Gulf of Mexico.

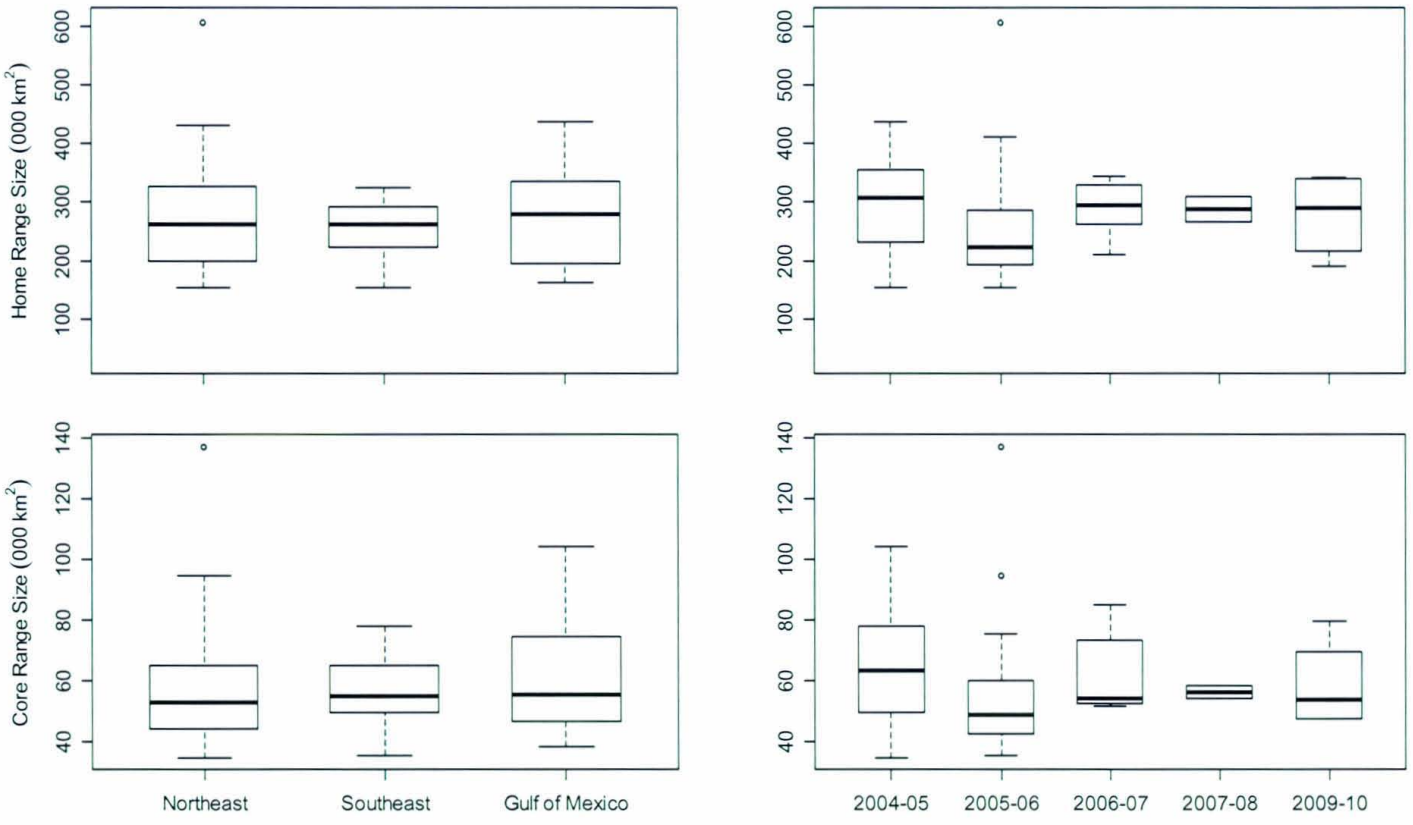

Figure 9. Home (95 %, top) and core (50 %, bottom) range sizes by winter destination (left) and year (right). Note the differing scales for home versus core range plots.

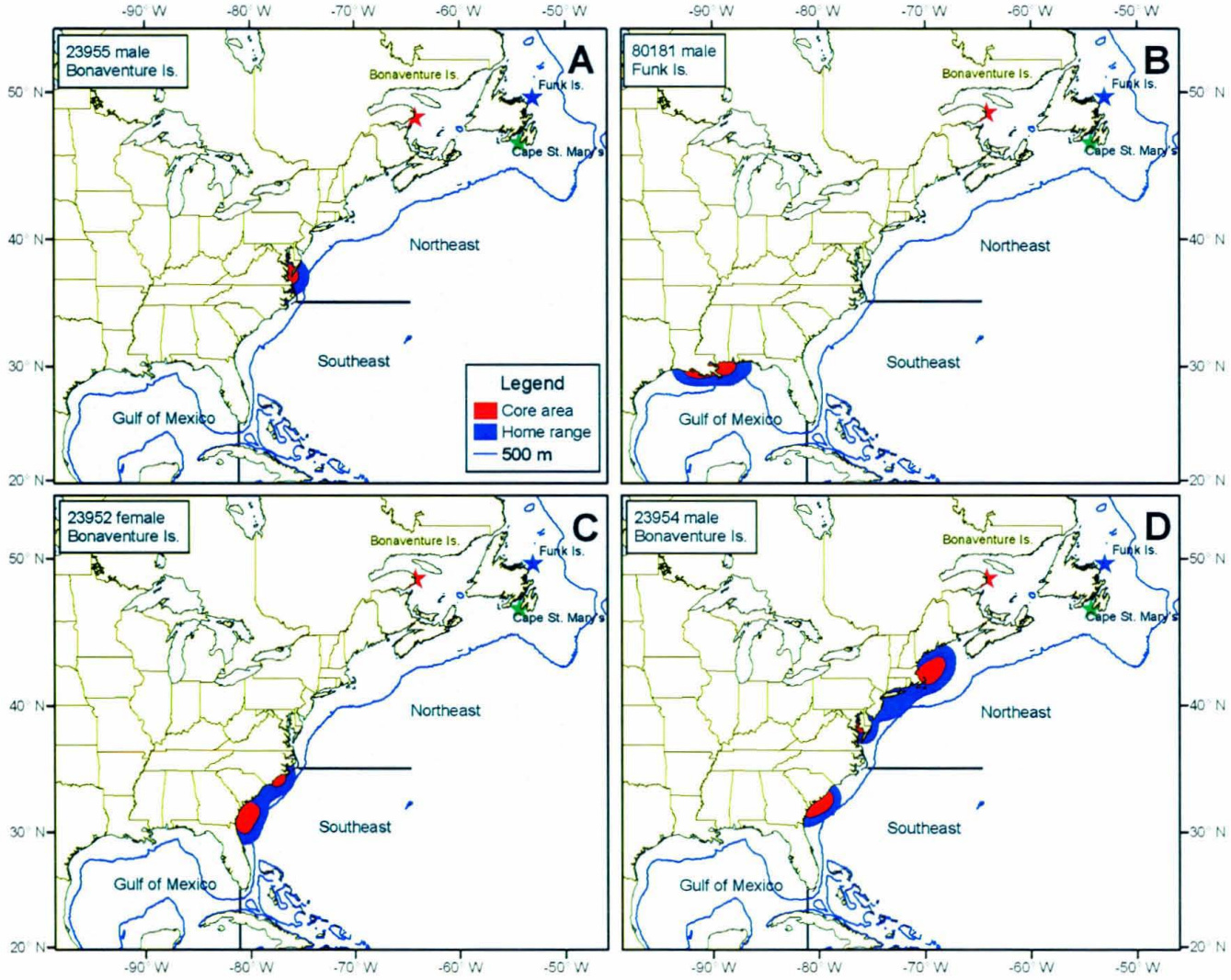
23955 male
Bonaventure Is.
A
80181 male
Funk Is.
B
23952 female
Bonaventure Is.
C
23954 male
Bonaventure Is.
D
Bonaventure Is.
Funk Is.
Cape St. Mary's
Northeast
Southeast
Gulf of Mexico
Legend
Core area
Home range
500 m
-90° W
-80° W
-70° W
-60° W
-50° W
50° N
40° N
30° N
20° N

Figure 10. Typical (A – C) North American winter (Jan – Feb) home and core ranges of Northern Gannets (*Morus bassanus*) showing restriction to a relatively small core geographical area. Atypical pattern (D) of one bird that ranged widely during Jan – Feb.

Neither home nor core range sizes differed among winter destinations, sexes or year (at Bonaventure Island; Table 5). There was weak support for Funk Island birds' home ranges being larger (76,698 ± 19,398 km^2 larger) in 2006-07 than in 2005-06 (Table 5). Home range sizes for the only other gannets tracked in 2006-07 (two from Cape St. Mary's) were similar to those for Funk Island (310,200 and 266,400 km^2). There was also weak support for a difference between colonies in 2005-06. In that year, Bonaventure Island home ranges were larger (61,514 ± 27,203 km^2) than those for Funk Island birds, although this difference disappeared when birds with the two largest home ranges at Bonaventure Island (gannets 23954 and 23959) were excluded ($F_{1,23} = 3.03$, $p = 0.1$; LMM). The most extreme bird, 23954, ranged widely (described above), while gannet 23959 had a winter home range that covered from the central Gulf of Maine to Cape Hatteras. Although the centroids for the mated pair were separated by roughly 730 km in 2005-06, a portion of their home ranges overlapped during Jan – Feb, but their overlap index (UDOI = 0.031) was extremely low indicating little likelihood of shared space use.

Table 5. Significance of terms in linear mixed-effect models for winter range sizes. Different columns represent different partitions of the data (see section 2.4). Winter destination and sex include all data for which these parameters were known, colony includes a comparison of Funk Island and Bonaventure Island in 2005-06, year columns compare 2004-05 with 2005-06 at Bonaventure Island, and 2005-06 with 2006-07 at Funk Island. Significant results are highlighted in bold.

Winter range	Colony	Winter destination	Year (Bonaventure Is.)	Year (Funk Is.)	Sex
Home (95 %)	**$F_{1,25} = 5.11$ p = 0.03**	$F_{2,14} = 0.22$, p = 0.80	$F_{1,10} = 0.99$, p = 0.34	**$F_{1,4} = 15.63$, p = 0.017**	$F_{1,29} = 0.16$, p = 0.70
Core (50 %)	$F_{1,25} = 2.13$, p = 0.16	$F_{2,14} = 0.04$, p = 0.96	$F_{1,10} = 0.71$, p = 0.42	$F_{1,4} = 3.74$, p = 0.13	$F_{1,29} = 1.02$, p = 0.32

3.1.3 Winter Site Fidelity

The wintering areas of most birds tracked to North American wintering areas in two consecutive years (n = 16) were remarkably consistent. All birds except one exhibited winter centroids in the same zone in consecutive years (Table 4, Figure 11). The median distance observed between consecutive winter centroids was only 87 km (range: 5 – 746 km), with nine birds having inter-centroid distances of less than 100 km. In contrast, the median distance between random pairings of centroids was 763 km. The observed distribution of inter-year centroid distances was significantly different than the randomized distribution ($D = 0.61$, $p < 0.0001$; KS test). Only four birds moved their winter centroid more than 200 km. One of these (gannet 23943) wintered in the southeast in 2004-05 and in the eastern Gulf of Mexico in 2005-06, another (gannet 23948) wintered further west in the Gulf of Mexico during 2004-05 than in 2005-06. One gannet (23955) wintered further north in the northeast zone in one year than the other, and gannet 23946 ventured into the southeast zone (as far as coastal Georgia) for part of the winter in one year but not the other. There was no detectable difference in the size of home (paired t-test, $t = -0.08$, $df = 15$, $p = 0.94$) or core (paired t-test, $t = 0.49$, $df = 15$, $p = 0.63$) ranges of individuals in consecutive years.

Home (all) and core (all except two) ranges overlapped for birds tracked in two years (Figure 12). Both core and home ranges overlaps were significantly greater than expected by chance. The median percentage of overlap in home and core ranges expected by chance alone (from randomized distributions) was 0 % (range: 0 – 100 %) for both year 1 overlapping on year 2 and year 2 overlapping on year 1. In contrast, the median

observed overlap of core ranges for year 1 on year 2 (39 %, range: 0 – 78 %) and for year 2 on year 1 (33 %, range: 0 to 87 %) were both significantly different than expected by chance ($D = 0.62$, $p < 0.0001$; KS test, $D = 0.62$, $p < 0.0001$; KS test, respectively). Likewise for home ranges, the median observed overlap was for year 1 on year 2 was 70 % (range: 0 – 96 %) ($D = 0.62$, $p < 0.0001$; KS test) and 60 % for year 2 on year 1 (range: 0 to 97 %) ($D = 0.66$, $p < 0.0001$; KS test).

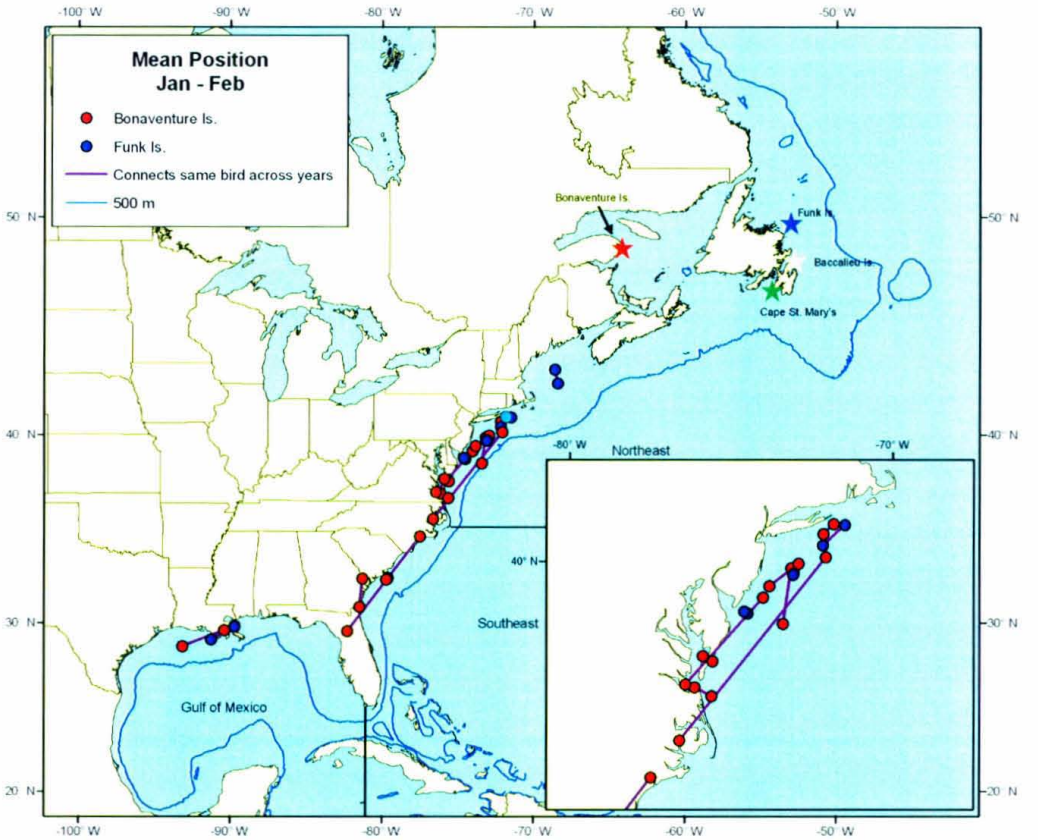

Figure 11. Inter-year consistency of winter (Jan – Feb) centroids of Northern Gannets (*Morus bassanus*) tracked in two consecutive years (n = 16). Purple lines connect the centroid locations of each bird between years. Inset presents close-up view of the region from Cape Cod to Cape Hatteras for clarity.

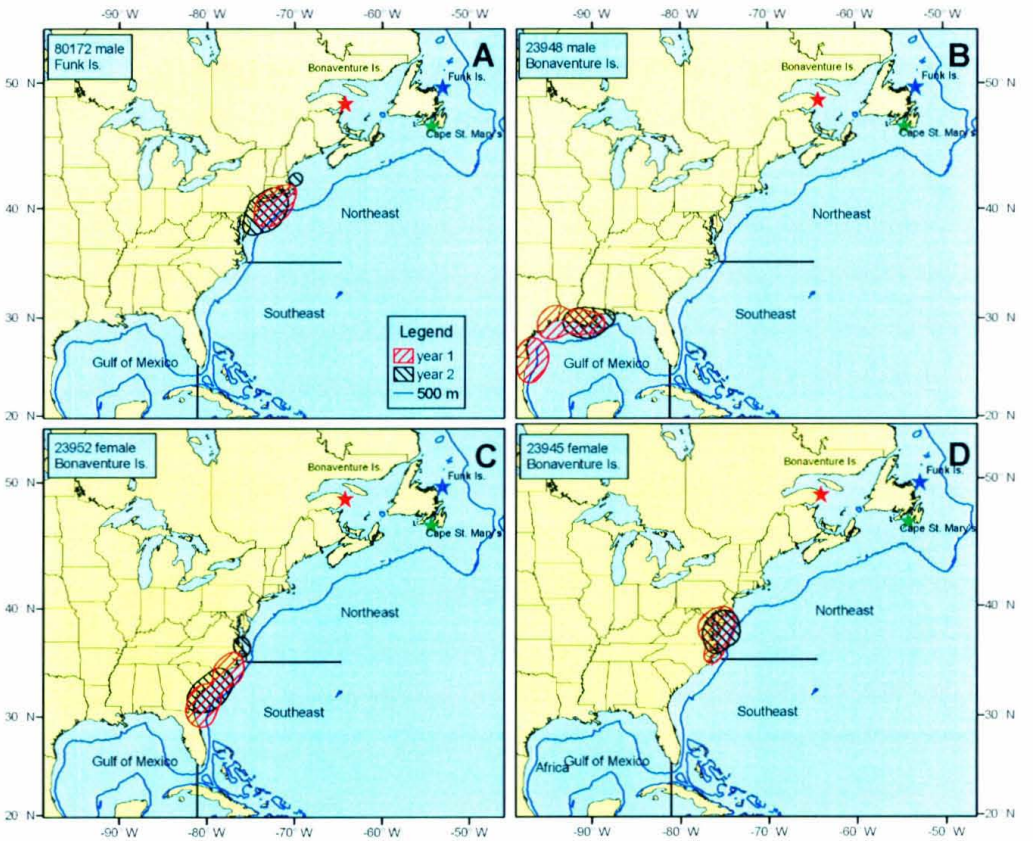

Figure 12. Typical home range overlap for Northern Gannets (*Morus bassanus*) tracked in two consecutive winters.

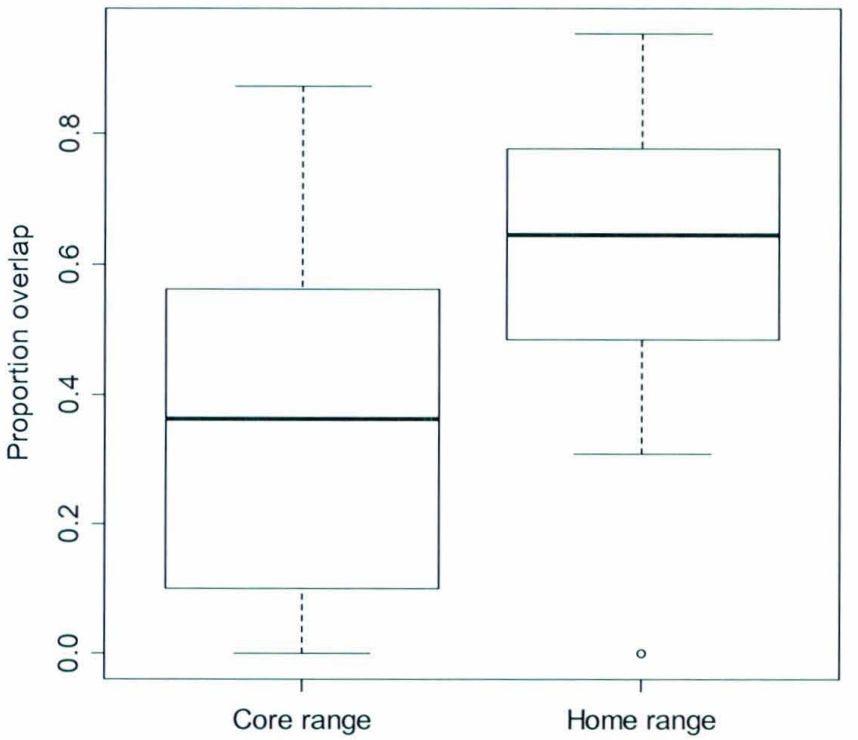

Figure 13. Proportion of overlap for core (50 %) and home (95 %) ranges for the same individual in consecutive years.

3.2 North American migration – timing and movement

Fifty-six complete fall (n = 40 individuals) and 51 complete spring (n = 37 individuals) migration tracks were recorded for gannets. Birds generally migrated over continental shelf waters, but some birds made occasional excursions into much deeper water (Figure 14).

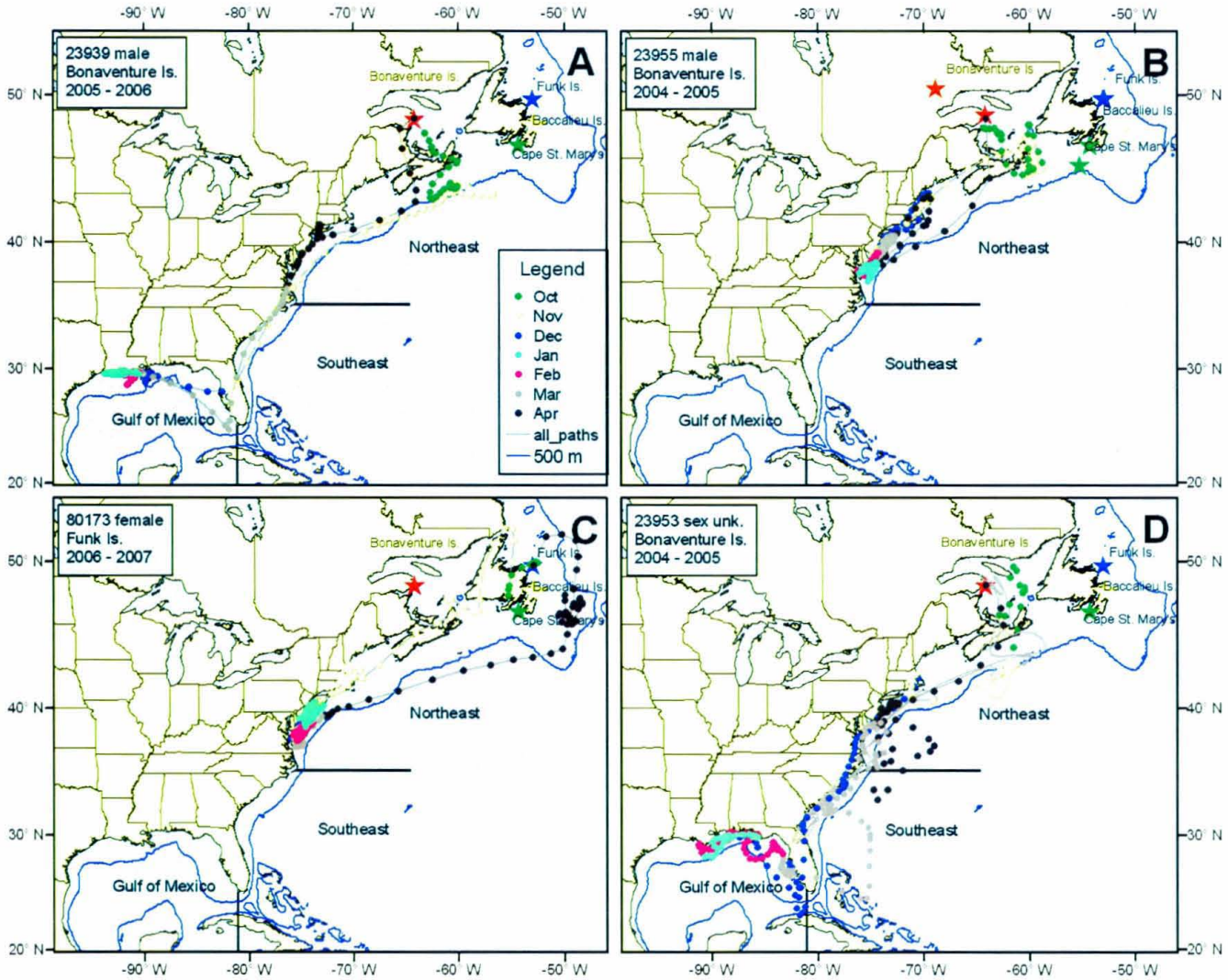
A
23939 male
Bonaventure Is.
2005 - 2006
B
23955 male
Bonaventure Is.
2004 - 2005
C
80173 female
Funk Is.
2006 - 2007
D
23953 sex unk.
Bonaventure Is.
2004 - 2005
Legend
Oct
Nov
Dec
Jan
Feb
Mar
Apr
all_paths
500 m
Northeast
Southeast
Gulf of Mexico
Bonaventure Is.
Funk Is.
Baccalieu Is.
Cape St. Mary's
-90° W
-80° W
-70° W
-60° W
-50° W
50° N
40° N
30° N
20° N

Figure 14. Migration routes of four individual geolocator-equipped Northern Gannets (*Morus bassanus*) showing (A) reasonably direct migration punctuated by significant fall stopover on the Scotian Shelf and a brief stop at Long Island in spring, (B) much shorter spring versus fall migration, (C) fall migration through the Strait of Belle Isle and along the west coast of Newfoundland with faster and more offshore spring migration, and (D) unusual extensive offshore excursions during spring migration. Dots represent bird positions (two per day), stars indicate colony locations.

3.2.1 Fall migration

Gannets departed their breeding colonies between 3 and 28 October (mean: 20 October ± 6 d, n = 55 departures from 39 individuals; Table 6; Figure 15) and moved south-westward along the eastern coast of North America, and for some, into the Gulf of Mexico. Eleven departures occurred during the first half of October and 44 occurred in the latter half of the month. There was great individual variability in the progress of movement towards wintering areas. Most October positions were north of Cape Cod but by the last week of the month some birds had reached Cape Hatteras (*ca.* 35°N, Figure 15) . During November, birds were distributed widely with some remaining near the breeding area while many occurred along the eastern North American coast. The earliest bird arrived at its (northeast zone) winter area on 8 November. Incredibly, one bird reached its winter area along the coast of Louisiana by 12 November. Gannets vacated the Gulf of St. Lawrence and the continental shelf waters of Newfoundland by mid-December, while in the Gulf of Mexico birds reached eastern Texas by early December. All birds (except 8) had finished their migration by 1 January and by the end of January the most distant had reached the Texas/Mexico border area. By then, the limit of their northern range had retracted to the Gulf of Maine and southern Scotian Shelf. Mean arrival date on the wintering grounds (4 December ± 21 d) was much more variable than colony departure date. The latest arrival on the wintering grounds occurred in the Gulf of Mexico on 4 February. The duration of the migratory period was also highly variable ranging from 12 to 110 days (mean: 46 ± 23 d). Birds had 23 ± 14 (range: 1.5 – 59.5) stopover days during fall migration with high stopover concentrations on the Scotian

Shelf (especially near Sable Island and The Gully), the mouth of the Bay of Fundy, the western Gulf of Maine, and the Delaware Bay/Chesapeake Bay region, with lesser concentrations on the Grand Bank and along the coast in the southeast zone (Figure 16). The distance travelled between colony departure and arrival on the winter grounds (including distance covered on stopover days) varied from 1,304 to 13,584 km (mean: 4,947 ± 2,500). There was a strong correlation between migration duration, distance, number of stopover days and migration end date (all Pearson $r > 0.7$). But, there was also considerable individual variation. For example, gannets wintering in the Gulf of Mexico had both the highest and lowest number of stopover days. The mean number of stopover days per day of migration was 0.48 ± 0.15 but ranged from 0.05 to 0.81. The smallest of these, a bird from Funk Island, migrated to the Gulf of Mexico in 28 days at a speed of 184 km d^{-1} with only 2 stopover days. Mean speed of migration was 110 ± 20 km d^{-1} (range: 71 – 184 km d^{-1}) and did not differ by date of departure ($F_{1,13} = 0.15$, $p = 0.70$; LMM). Time spent in the winter area varied from 48 to 152 days (mean: 118 ± 26 d, median: 125 d).

Table 6. Fall and spring migration parameters (n = 56 trips from 39 individuals) for Northern Gannets (*Morus bassanus*) wintering in North America.

	Mean ± SD	Range
Fall		
Start date[1]	20 Oct ± 6	3 Oct – 28 Oct
End date	4 Dec ± 21	8 Nov – 4 Feb
Duration (d)	46 ± 23	12 – 110
Stopovers (d)	23 ± 14	1.5 – 59.5
Distance (km)	4,947 ± 2,500	1,304 – 13,584
Speed (km d^{-1})	110 ± 20	71 – 184
Days in winter area	118 ± 26	48 – 152
Spring		
Start date	29 Mar ± 14	22 Feb – 25 Apr
End date	22 Apr ± 6	5 Apr – 4 May
Duration (d)	24 ± 14	2 – 64
Stopover (d)	11 ± 8	0.5 – 32.5
Distance (km)	3,408 ± 1,840	619 – 9,461
Speed (km d^{-1})	164 ± 72	84 – 486

[1]Number of trips for fall start date is 55 and number of individuals is 39 since one bird lost its chick and departed early.

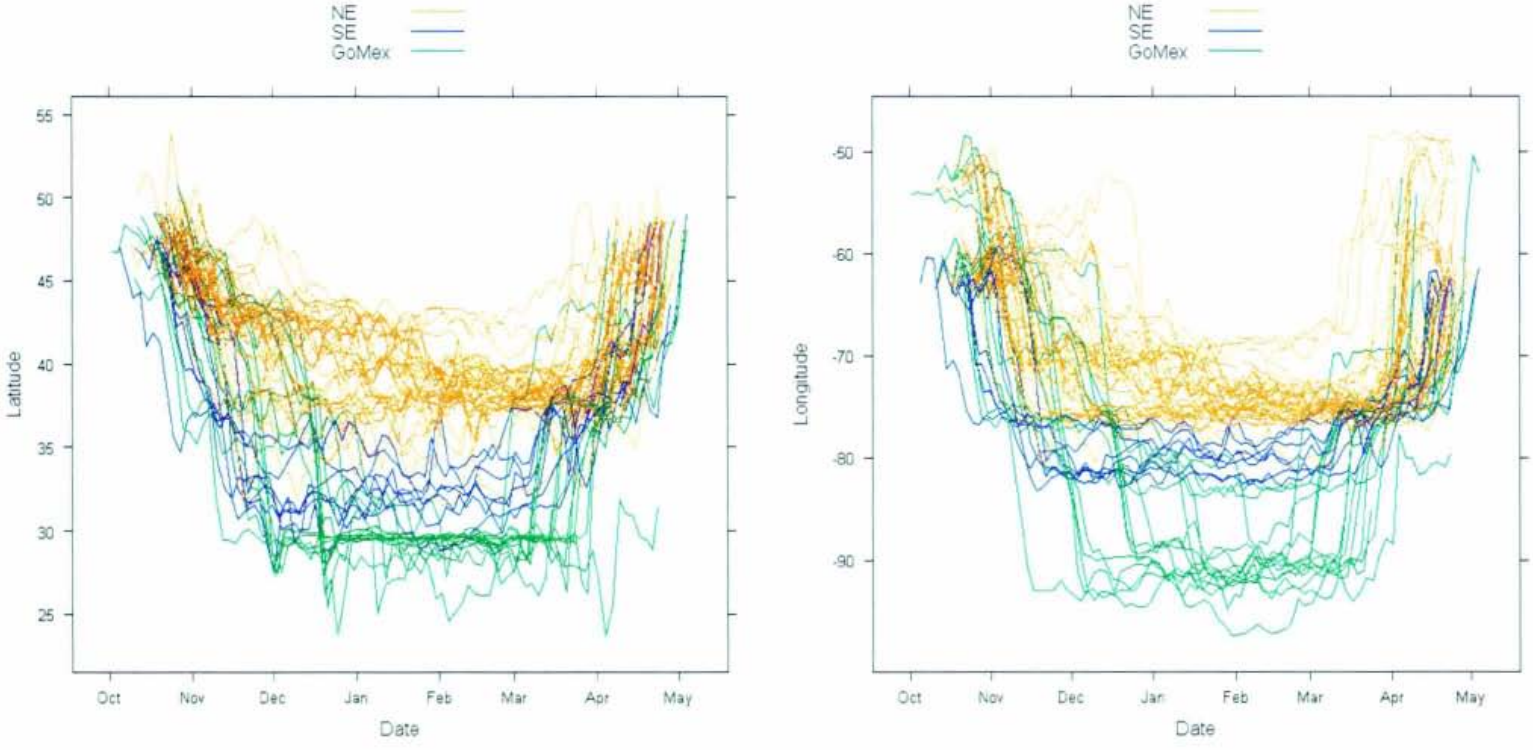

Figure 15. Latitude (A) and longitude (B) averaged over 5 days for North American migrations of geolocator-equipped Northern Gannets (*Morus bassanus*) coloured by winter destination. NE = northeast, SE = southeast, GoMex = Gulf of Mexico.

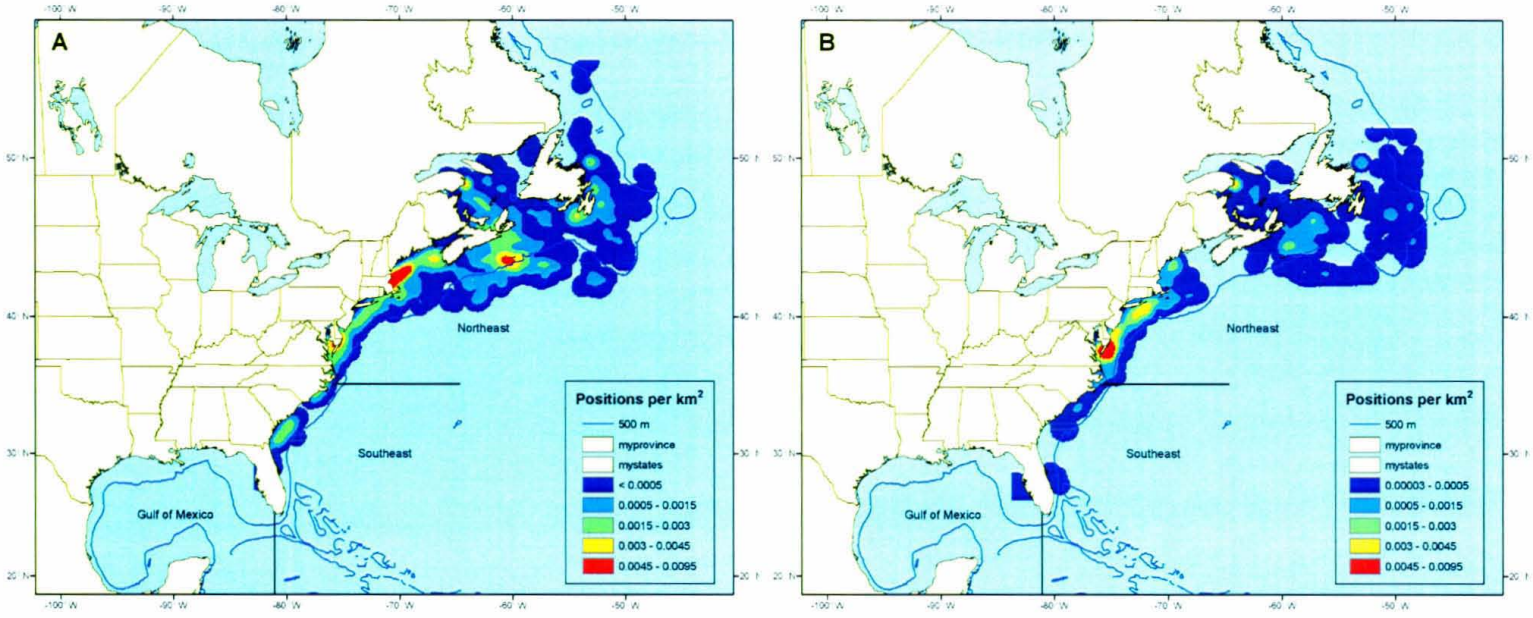

Figure 16. Maps of (A) fall and (B) spring density of stopover days for Northern Gannet (*Morus bassanus*) migrations in North America.

3.2.2 Spring migration

Initiation of spring migration ranged from 22 February to 25 April (mean: 29 March ± 14 d, n = 51 trips from 37 individuals; Table 6; Figure 15). Only one departure from the winter grounds occurred in February with the rest occurring in March (n = 25) and April (n = 25). By the last two weeks of March the earliest birds had reached the Scotian Shelf and Grand Bank (n = 8 trips). By 2 April all birds had vacated the Gulf of Mexico and by the third week of April all positions were north of Cape Hatteras. Colony arrival date was less variable than departure from the winter area. Arrival for six trips occurred during the first two weeks of April, for 41 trips during the last two weeks of April and 4 occurred during the first week of May producing a mean colony arrival date of 22 April ± 6 d, range: 5 April – 4 May. The duration of spring migration varied from 2 to 64 d with a mean of 24 ± 14 d and involved 11 ± 8 (range: 0.5 – 32.5) stopover days en route. Seven birds had no stopover days during spring migration. Important stopover areas during spring migration included the Delaware Bay/Chesapeake Bay region, the area southeast of Long Island, and to a lesser extent the western Gulf of Maine and Scotian Shelf (Figure 16). Surprisingly, geolocator temperature data revealed that several birds spent one or more nights on land in the vicinity of Sable Island, suggesting they roosted on this offshore island. The mean number of stopover days per day of migration was similar to fall at 0.42 ± 0.18 (range: 0.02 – 0.80). The distance covered during spring migration (including distances moved on stopover days) was 3,408 ± 1,840 km (range: 619 – 9,641 km) at an overall speed of 164 ± 72 km d^{-1} (range: 84 – 486 km d^{-1}). Migrations initiated later in spring were 1.9 ± 0.8 days faster per day of delayed departure

than those initiated earlier ($F_{1,11} = 5.43$, $p = 0.04$; LMM). There was little evidence that return migrations were further offshore than in fall; only 16 of 51 spring migrations were clearly more offshore than in fall, the others overlapped partially or completely.

3.2.3 Colony comparison

There was little evidence of colony-specific differences in migration parameters between Bonaventure Island and Funk Island in 2005-06 (Table 7; Table 8). One exception, contrary to prediction, was that birds returned to Funk Island 11 ± 2s days earlier in spring than at Bonaventure Island in 2005-06. Colony arrival at Funk Island in this year was also earlier than in the subsequent year (see section 3.2.6).

Table 7. Colony comparison of Northern Gannet (*Morus bassanus*) migration parameters between Bonaventure Island (Fall n = 20, Spring n = 19) and Funk Island (Fall n = 7, Spring n = 6) during 2005-06. Significant differences are shown in bold, statistics and p-values are presented in Table 8.

	Bonaventure Island		**Funk Island**	
	Mean ± SD	Range	Mean ± SD	Range
Fall				
Start date	19 Oct ± 7	3 Oct – 27 Oct	16 Oct ± 5	10 Oct – 22 Oct
End date	28 Nov ± 17	8 Nov – 3 Jan	3 Dec ± 17	9 Nov – 21 Dec
Duration (d)	40 ± 17	12 – 82	47 ± 18	28 – 72
Stopovers (d)	21 ± 12.5	3 – 48	21 ± 11	2 – 32
Distance (km)	4,320 ± 1,667	1,304 – 7,224	5,524 ± 1,900	3,408 – 8,655
Speed (km d^{-1})	110 ± 17	81 – 135	121 ± 31	84 – 184
Spring				
Start date	30 Mar ± 11	13 Mar –19 Apr	21 Mar ± 13	3 Mar – 2 Apr
End date	**24 Apr ± 4**	**17 Apr – 3 May**	**13 Apr ± 6**	**5 Apr – 20 Apr**
Duration (d)	25 ± 13	7 – 49	23 ± 13	6 – 40
Stopovers (d)	11 ± 7	0.5 – 24.5	10 ± 9	0 – 23
Distance (km)	3,223 ± 1,426	1,365 – 5,702	3,823 ± 1,338	1,867 – 5,133
Speed (km d^{-1})	137 ± 29	102 – 218	189 ± 62	119 – 287

Table 8. Significance of migration parameters in linear mixed-effect models. Different columns represent different partitions of the data (see section 2.4). Winter destination and sex include all data for which these parameters were known, colony includes a comparison of Funk Island and Bonaventure Island in 2005-06, year columns compare 2004-05 with 2005-06 at Bonaventure Island, and 2005-06 with 2006-07 at Funk Island. Significant results are highlighted in bold

	Colony		**Winter destination**		**Year (Bonaventure Is.)**		**Year (Funk Is.)**		**Sex**	
Fall	$F_{1,25}$	**P**	$F_{2,14}$	**P**	$F_{1,10}$	**P**	$F_{1,4}$	**P**	$F_{1,29}$	**P**
Start date	0.75	0.39	**3.75**	**0.05**	**5.00**	**0.049**	7.16	0.06	**8.80**	**0.006**
End date	0.34	0.56	**12.45**	**0.0008**	0.47	0.51	1.61	0.27	0.02	0.88
Duration	0.82	0.37	**16.01**	**0.0002**	0.05	0.83	0.19	0.69	0.51	0.48
Stopover	0.004	0.95	**10.38**	**0.0017**	0.01	0.91	< 0.01	0.99	0.18	0.68
Distance	2.53	0.12	**14.06**	**0.0004**	0.12	0.74	2.06	0.22	1.34	0.26
Speed	0.86	0.36	**16.42**	**0.0004**	0.20	0.66	0.84	0.41	0.02	0.90
Spring	$F_{1,23}$	**P**	$F_{2,12}$	**P**	$F_{1,8}$	**P**	$F_{1,4}$	**P**	$F_{1,28}$	**P**
Start date	3.25	0.08	**21.11**	**0.0001**	0.002	0.97	1.85	0.24	0.003	0.96
End date	**25.64**	**< 0.0001**	0.40	0.68	0.004	0.95	**17.47**	**0.014**	3.16	0.09
Duration	0.07	0.80	**21.10**	**0.0001**	0.03	0.87	2.27	0.21	0.06	0.81
Stopovers	0.03	0.85	**10.00**	**0.003**	0.25	0.63	0.26	0.63	0.02	0.88
Distance	0.83	0.37	**14.51**	**0.0006**	1.46	0.26	1.01	0.37	0.07	0.79
Speed	4.00	0.06	**5.00**	**0.03**	2.50	0.15	1.53	0.28	0.50	0.48

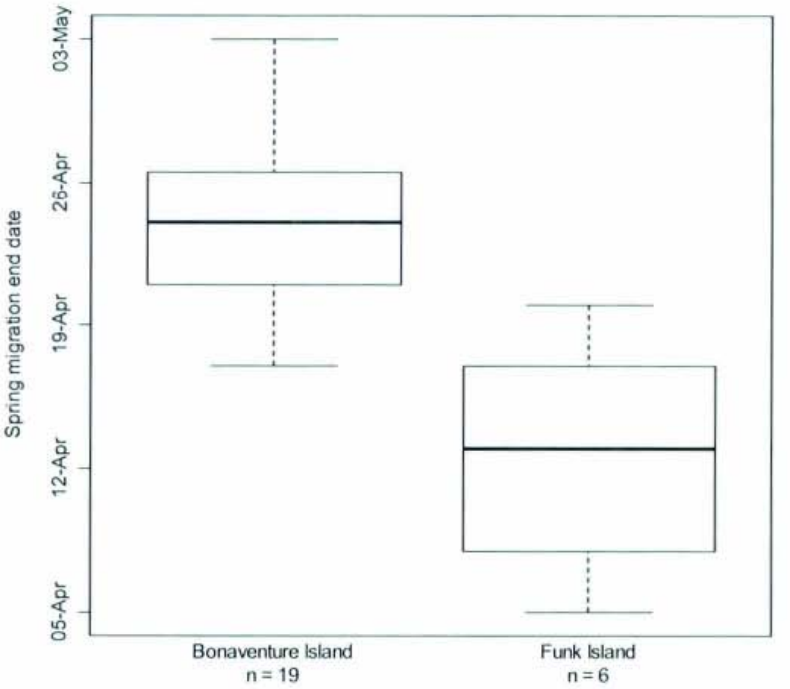

Figure 17. Date of spring colony return for Northern Gannets (*Morus bassanus*) at Bonaventure Island and Funk Island in 2006.

3.2.4 Destination comparison

Winter destination had a significant effect on most timing and movement parameters for both the fall and spring migrations (Table 8).

Fall migration. In comparison to the northeast, trips to the Gulf of Mexico departed on similar dates, but took 27 ± 7 days longer, covered greater distance (3,686 ± 765 km) travelling at a faster speed (18 ± 7 km d^{-1}) and, contrary to prediction, they used a similar number of stopover days (Figure 18). Expectedly, the gannet with the shortest

distance (1,304 km) wintered in the northeast zone and the one with the longest distance (13,584 km) in the Gulf of Mexico but, the gannet with the second longest distance (11,778 km) wintered in the northeast zone. It made a trip to the central Labrador shelf immediately after colony departure, vastly increasing its migration distance.

Surprisingly, migration parameters for trips to the southeast were not intermediate between those for the northeast and the Gulf of Mexico (Figure 18). Instead, in comparison to the northeast, they had earlier fall departure dates (weak evidence), covered similar distances during similar migration durations by taking less circuitous routes at a faster (25 ± 4 km d^{-1}) speed using 9.5 ± 3 fewer stopover days (Figure 18). In comparison to the Gulf of Mexico, trips to the southeast departed on similar dates, took 41 ± 8 fewer days, covered 4,173 ± 1,060 fewer kilometres at a similar speed and used 17 ± 4.5 fewer stopover days (Figure 18). All trips to the southeast (n = 7) were made by gannets from Bonaventure Island (n = 5), but they occurred over 2 years (2004-05: 2 birds, 2005-06: 5 birds) and involved 3 males and 2 females. There was considerable overlap in the speed of migration among the destinations, but seven of the top 10 fastest (speed wise) migrations were either to the Gulf of Mexico or the southeast zone.

Spring migration. In contrast to fall, spring migration conformed better to expectations. In most cases, the southeast was intermediate between the northeast and the Gulf of Mexico and more similar to the latter. There were significant differences between one or more winter zones in all measured parameters, except arrival date, (Table 5) and the greatest differences were between the most widely separated areas (i.e. northeast versus Gulf of Mexico; Figure 19). Spring migrations between nearer (to the colony) and

more distant zones included earlier departure (GoMex vs NE: 24 ± 4 d; SE vs NE: 16 ± 4 d), longer migration duration (GoMex vs NE: 24 ± 4 d; SE vs NE: 16 ± 5 d), greater travel distances (GoMex vs NE: 3,373 ± 653 km; SE vs NE: 1,415 ± 621 km) at similar speeds (except SE vs NE: 53 ± 17 km d^{-1} slower) using more stopover days (GoMex vs NE: 10 ± 2.5 d; SE vs NE: 7.5 ± 3 d). In contrast to fall migration, the top 10 fastest (speed wise) spring migrations were all by birds from the northeast zone except one migrating from the Gulf of Mexico (the same bird that had the fastest migration in fall).

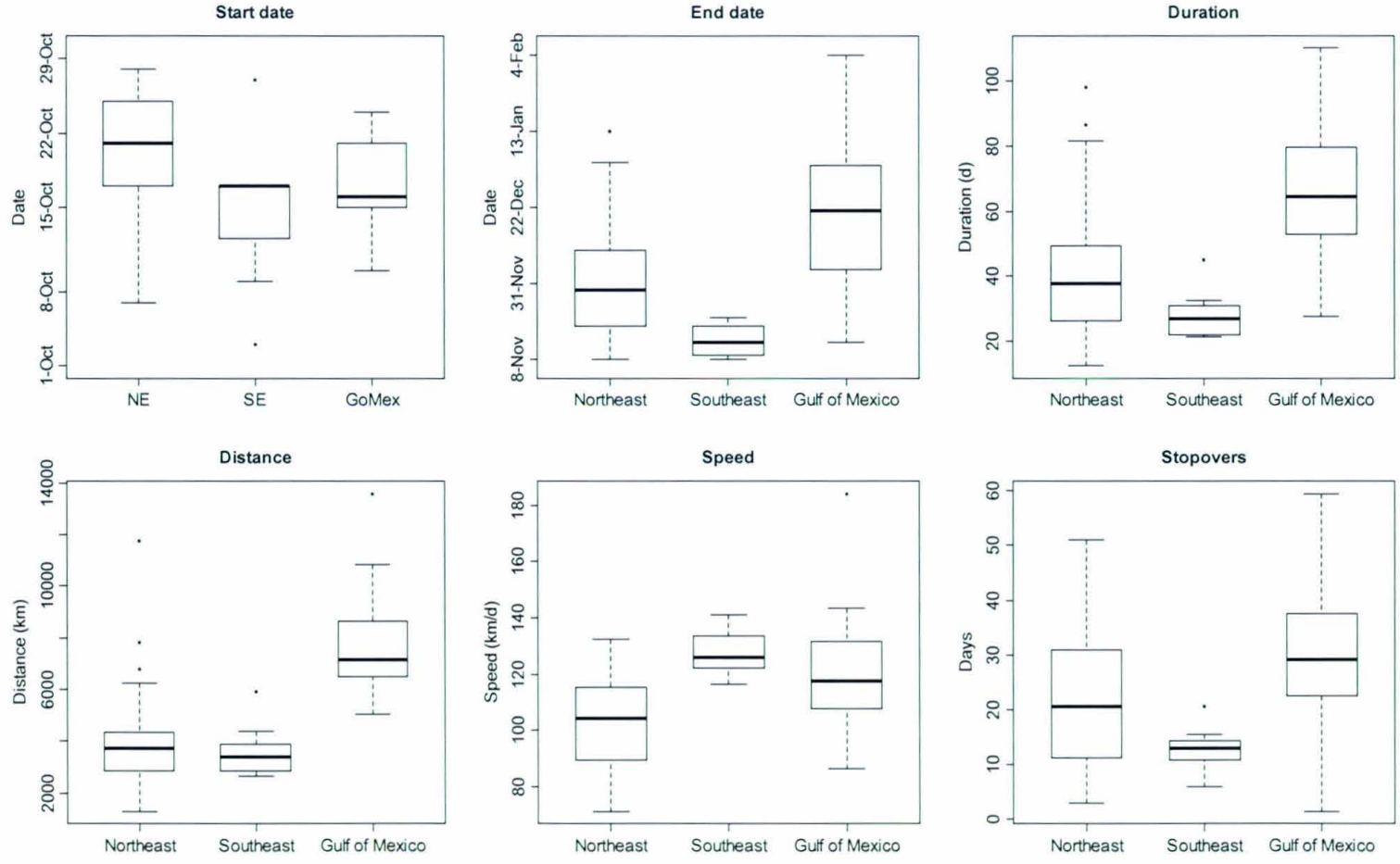

Figure 18. Boxplots of fall migration parameters by winter destination for Northern Gannets (*Morus bassanus*). Samples sizes are northeast = 35, southeast = 7, Gulf of Mexico = 14 except for start date where Gulf of Mexico = 13.

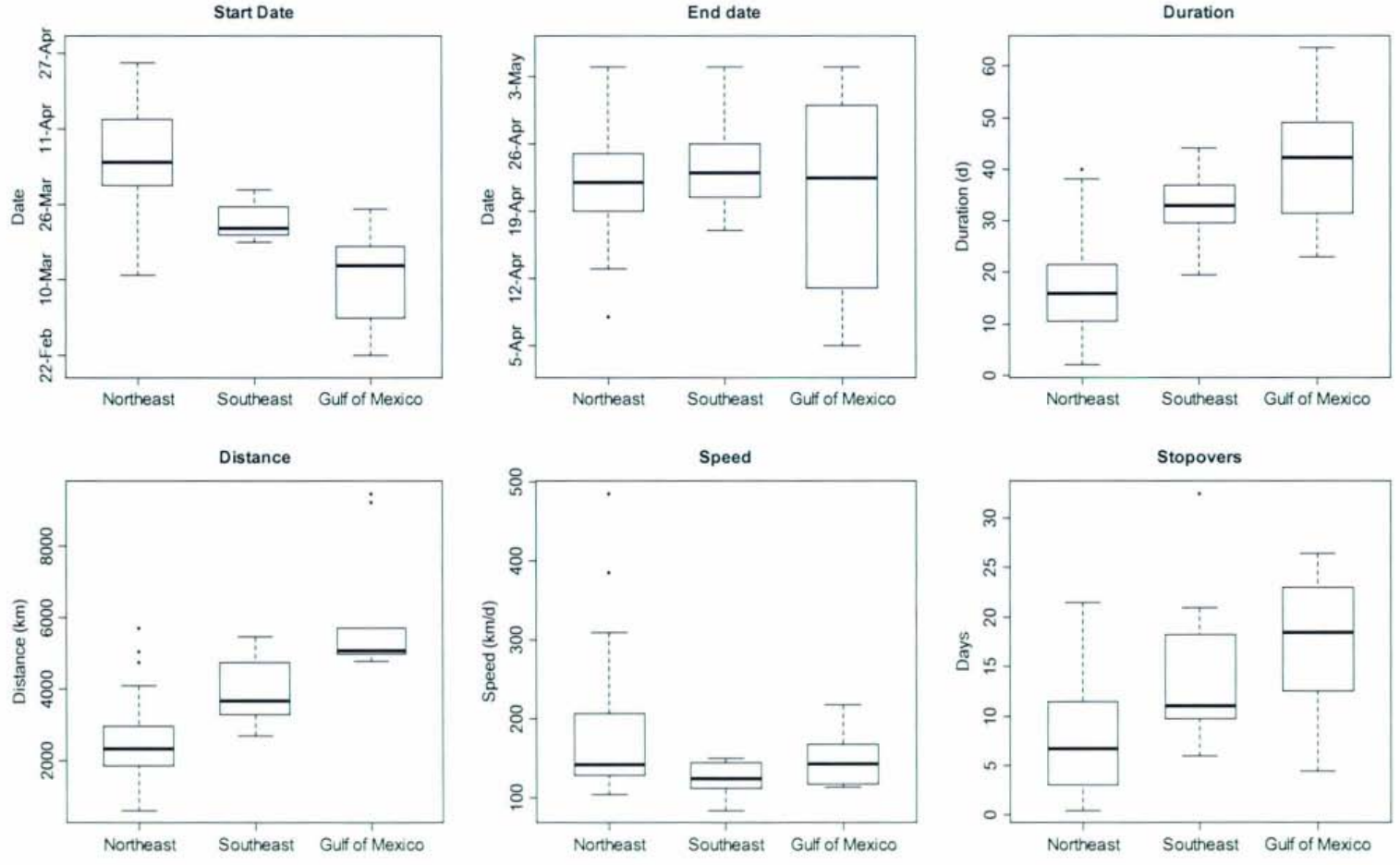

Figure 19. Boxplots of spring migration parameters by winter destination for Northern Gannets (*Morus bassanus*). Samples sizes are Northeast = 34, Southeast = 7, Gulf of Mexico = 10.

3.2.5 Sex comparison

Only colony departure date was significantly different between the sexes; males departed the colony 5 ± 2 days later than females (Table 8; Table 9). In the only mated pair tracked, the male departed 6 and 11 days later than the female in 2004 and 2005, respectively. Contrary to prediction, males and females did not return to the colony at significantly different dates in spring, instead both sexes had similar mean (both 22 April), earliest (5 April versus 8 April) and latest (both 4 May) arrival dates (Table 9). This result did not change when each colony was examined individually in each year (all $p > 0.42$). The male of the mated pair returned 3 days before the female in 2006.

Table 9. Sex comparison of Northern Gannet (*Morus bassanus*) migration parameters (fall female n = 14, fall male n = 33, spring female n = 13, spring male n = 31). Significant differences are shown in bold, statistics and p-values are presented in Table 8.

	Females		Males	
	Mean ± SD	Range	Mean ± SD	Range
Fall				
Start date	**17 Oct ± 7**	**3 Oct – 26 Oct**	**22 Oct ± 5**	**10 Oct – 28 Oct**
End date	27 Nov ± 19	7 Nov – 12 Jan	3 Dec ± 17	8 Nov – 12 Jan
Duration (d)	42 ± 19	22 – 86	43 ± 19	12 – 82
Stopovers (d)	19.5 ± 12.5	4.5 – 51	22 ± 13	1.5 – 48
Distance (km)	4,601 ± 1,983	2,580 – 8,655	4,390 ± 1,760	1,304 – 9,328
Speed (km d^{-1})	114 ± 17	77 – 132	107 ± 23	71 – 184
Spring				
Start date	31 Mar ± 10	15 Mar – 17 Apr	30 Mar ± 14	2 Mar – 25 Apr
End date	22 Apr ± 7	8 Apr – 4 May	22 Apr ± 6	5 Apr – 4 May
Duration (d)	22 ± 15	4 – 49	23 ± 13	2 – 64
Stopovers (d)	10.5 ± 10.5	0.5 – 32.5	10.5 ± 6	0.5 – 23
Distance (km)	3,119 ± 1,362	1,257 – 5,702	3,283 ± 1,850	619 – 9,461
Speed (km d^{-1})	188 ± 85	84 – 385	159 ± 72	103 – 486

3.2.6 *Year comparison*

There was weak evidence that birds departed Bonaventure Island later in 2004-05 than 2005-06 and marginal evidence for a similar pattern at Funk Island between 2005-06 and 2006-07. Birds also returned to Funk Island earlier in 2005-06 than in 2006-07 (Table 8; Table 10; Table 11). There was no evidence for a difference between years for any other migration parameters. There was greater synchrony in departure and arrival dates at a given colony in a given year than in the data set as a whole. The range from the earliest to the latest fall departure date for all migrations combined was 26 days, whereas for individual colonies in each year this difference ranged from 0 to 19 days. Likewise, the range in spring colony arrival date across all birds spanned 29 days, whereas colony/year specific ranges were between 3 and 18 days.

Table 10. Comparison of migration parameters of Northern Gannets (*Morus bassanus*) for 2004-05 versus 2005-06 at Bonaventure Island (fall 2004-05 n = 17, fall 2005-06 n = 20, spring 2004-05 n = 15, spring 2005-06 n = 19). Significant differences are shown in bold, statistics and p-values are presented in Table 8.

	2004-05		2005-06	
	Mean ± SD	Range	Mean ± SD	Range
Fall				
Start date	**23 Oct ± 5**	**9 Oct – 28 Oct**	**19 Oct ± 7**	**3 Oct – 27 Oct**
End date	4 Dec ± 20	8 Nov – 18 Jan	28 Nov ± 17	8 Nov – 3 Jan
Duration (d)	43 ± 23	22 – 102	40 ± 17	12 – 82
Stopovers (d)	22 ± 13.5	4.5 – 45	21 ± 12.5	3 – 48
Distance (km)	4,540 ± 2,834	2,518 – 13,584	4,320 ± 1,667	1,304 – 7,224
Speed (km d^{-1})	107 ± 23	71 – 143	110 ± 17	81 – 135
Spring				
Start date	3 Apr ± 15	1 Mar – 25 Apr	30 Mar ± 11	13 Mar – 19 Apr
End date	23 Apr ± 5	16 Apr – 4 May	24 Apr ± 4	17 Apr – 3 May
Duration (d)	21 ± 15	2 – 55	25 ±13	7 – 49
Stopovers (d)	11 ± 9	0.5 – 32.5	11 ± 7	0.5 – 24.5
Distance (km)	3,014 ± 2,114	619 – 9,205	3,223 ± 1,426	1,365 – 5,702
Speed (km d^{-1})	182 ± 103	84 – 486	137 ± 29	102 – 218

Table 11. Comparison of migration parameters of Northern Gannets (*Morus bassanus*) for 2005-06 versus 2006-07 at Funk Island (fall 2005-06 n = 7, fall 2006-07 n = 6, spring 2005-06 n = 6, spring 2006-07 n = 6). Significant differences are shown in bold, statistics and p-values are presented in Table 8.

	2005-06		2006-07	
	Mean ± SD	Range	Mean ±SD	Range
Fall				
Start date	16 Oct ± 5	10 Oct – 22 Oct	22 Oct ± 3	18 Oct – 26 Oct
End date	3 Dec ± 17	9 Nov – 21 Dec	8 Dec ± 23	15 Nov – 1 Dec
Duration (d)	47 ± 18	28 – 72	46 ± 23	22 – 80
Stopovers (d)	20.5 ± 11	1.5 – 31.5	21 ± 15.5	7.5 – 48
Distance (km)	5,524 ± 1900	3,408 – 8,655	4,912 ± 2,368	2,740 – 9,328
Speed (km d^{-1})	121 ± 31	84 – 184	108 ± 16	84 – 122
Spring				
Start date	21 Mar ± 13	3 Mar – 2 Apr	25 Mar ± 16	2 Mar – 14 Apr
End date	13 Apr ± 6	5 Apr – 20 Apr	26 Apr ± 4	21 Apr – 4 May
Duration (d)	23 ± 13	6 – 40	32 ±18	12 – 64
Stopovers (d)	10 ± 9.5	0.5 – 23	12.5 ± 5.5	4 – 19
Distance (km)	3,823 ± 1,338	1,867 – 5,133	4,886 ± 2,607	2,040 – 9,461
Speed (km d^{-1})	189 ± 62	119 – 287	156 ± 23	133 – 195

3.2.7 Fall versus spring migration

Spring migration routes generally retraced those of fall and, contrary to prediction, only 16 of 51 complete round-trip migrations had significant portions of the spring migration more offshore than during fall. Overall, spring migrations were faster and shorter than fall migrations. Spring migrations were 21 ± 3 days shorter ($F_{1,66}$ = 50.08, $p < 0.0001$), covered 1,277 ± 269 fewer km ($F_{1,66}$ = 26.06, $p < 0.0001$) at 54 ± 10 km d^{-1} faster speed ($F_{1,66}$ = 34.05, $p < 0.0001$) and used 12 ± 2 fewer stopover days ($F_{1,66}$ = 22.49, $p < 0.0001$; Figure 20). However, the number of stopover days per day of migration was quite similar (0.48 ± 0.15 versus 0.42 ± 0.15). This overall pattern did not

differ between males and females (all p-values > 0.25). But, it did differ depending upon winter destination for all parameters (all interactions of season and destination, $p < 0.01$). Inspection of interaction plots (Figure 21) showed that the difference between fall and spring migrations to/from the northeast and Gulf of Mexico were consistent for all parameters, whereas the difference between fall and spring migrations to/from the southeast did not follow the same pattern. In all cases (except speed), spring migration parameters for the southeast zone were intermediate between those for trips migrating from the northeast and Gulf of Mexico as expected (Figure 21). The lack of consistency with the other two zones was due to the uncharacteristically fast and short migrations to the southeast in fall (described in section 3.2.4).

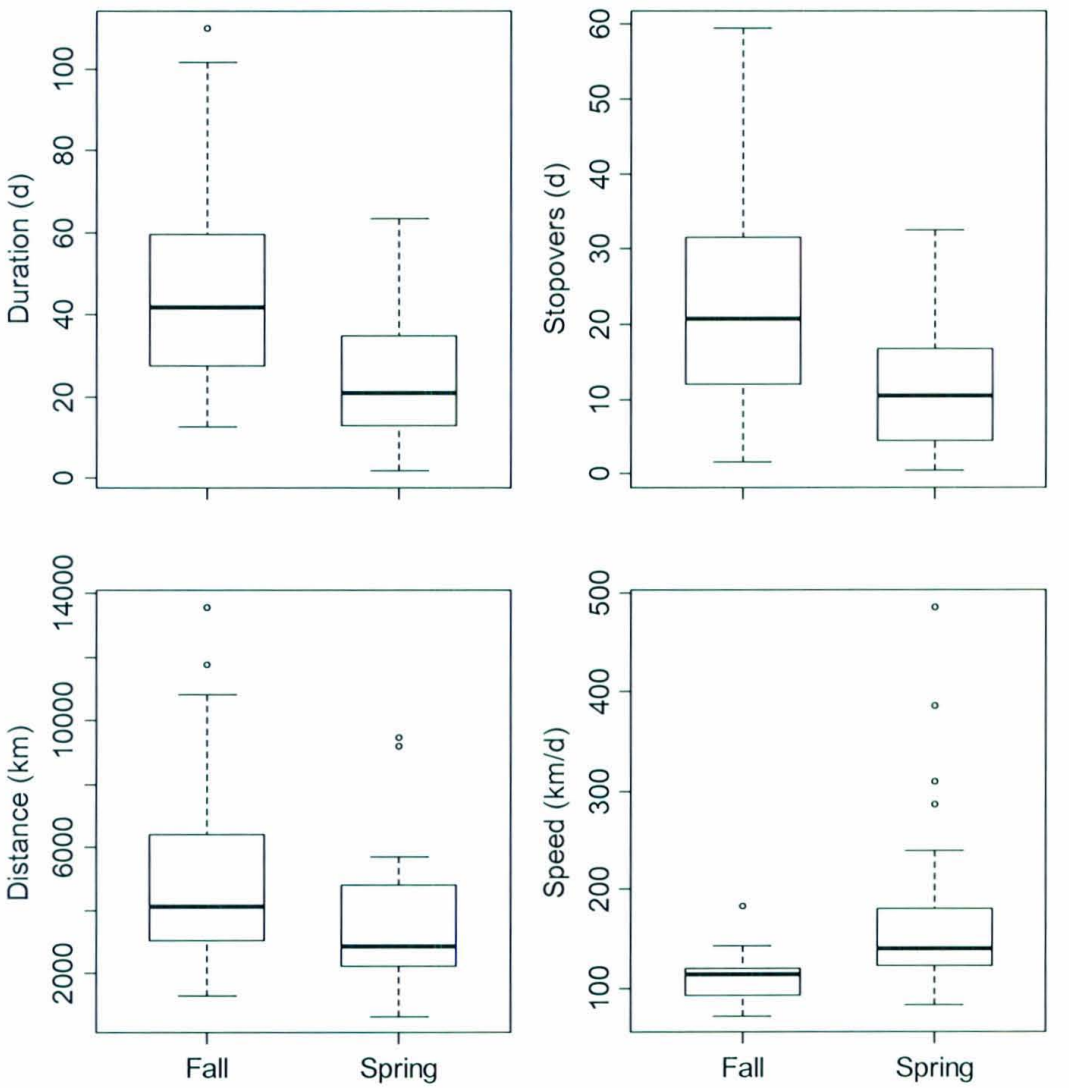

Figure 20. Comparison of fall and spring migration parameters for Northern Gannets (*Morus bassanus*).

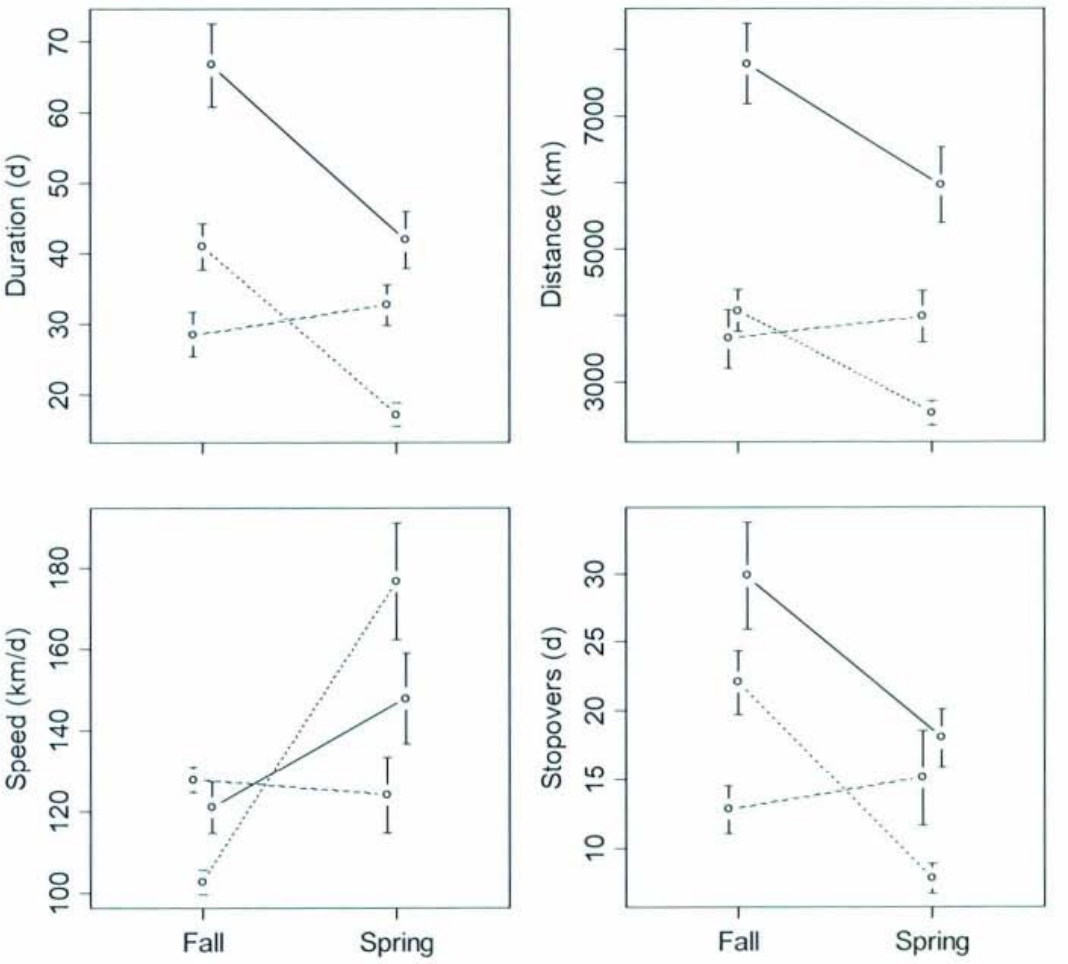

Figure 21. Interaction plots of spring and fall migration parameters versus winter destination for Northern Gannets (*Morus bassanus*). Dotted lines = northeast, dashed lines = southeast, solid lines = Gulf of Mexico.

3.2.8 Migration consistency

In the population as a whole, there was no indication that individuals shifted the timing of their migratory movements in successive years (paired t-tests, all p-values > 0.05). However, repeatability scores were only significant for certain timing parameters (Table 12). All migration parameters showing significant repeatability had r scores $\geq$ 0.42. Fall migration end date, duration and distance, all of which are highly correlated (Pearson $r \geq 0.8$), exhibited significant repeatability. Similarly, spring departure date, duration and distance showed significant repeatability within individuals; again these three parameters are highly correlated (Pearson $r \geq 0.9$). These results did not change when colonies were considered separately, except that spring colony arrival date was significantly repeatable for Bonaventure Island birds ($r = 0.59$, $F_{8,9} = 3.97$, $p = 0.03$), but not for Funk Island birds ($r < 0.01$, $F_{4,5} = 0.099$, $p = 0.98$).

Table 12. Repeatability of migration behaviours between years for Northern Gannets (*Morus bassanus*). Significant results are shown in bold.

Parameter	*r*	F	P
Fall (n = 16)			
Start date	<0.01	0.94	0.55
End date	**0.42**	**2.47**	**0.04**
Duration (d)	**0.42**	**2.47**	**0.04**
Stopovers (d)	0.30	1.78	0.13
Distance (km)	**0.61**	**4.08**	**0.004**
Speed (km d^{-1})	0.32	1.92	0.1
Spring (n = 14)			
Start date	**0.90**	**17.41**	**< 0.0001**
End date	<0.01	0.84	0.62
Duration (d)	**0.75**	**6.87**	**0.0005**
Stopovers (d)	0.37	2.20	0.08
Distance (km)	**0.64**	**4.59**	**0.004**
Speed (km d^{-1})	<0.01	0.93	0.55

3.3 Trans-Atlantic migration

3.3.1 Bands

Nine recoveries of gannets banded in North America (Table 13) occurred in the eastern Atlantic (Gaston et al. 2008). Most (n = 6) were recovered as immature birds, though three were adults. Gannets from Funk Island were recovered in Iceland, Ireland, Portugal, Morocco and Madeira while the single (immature) gannet from Bonaventure Island was recovered in northern Spain (Figure 22). Birds banded as chicks comprised the most Atlantic-crossing gannets (6 of 8 at Funk Island, 1 at Bonaventure Island), and four recoveries occurred in the first year of life (all from Funk Island; Table 13). Most

recoveries occurred during the non-breeding season except for two fledglings banded at Funk Island: one banded in August 1986 and recovered in Morocco one month later, and one banded in August 1984 and recovered as an adult in Iceland in May 1991. About five times more gannets have been banded in eastern Atlantic colonies (n = 62,328 banded, 3,218 recoveries; Wanless 2002) compared to North America (n = 13,494 banded, 832 recoveries; Table 14). Yet, not a single gannet banded in the eastern Atlantic Ocean has been recovered in the western Atlantic Ocean. The difference in the frequency of Atlantic crossings by North American (9 of 832) versus European (0 of 3,218) gannets is remarkable (Fisher exact test, $p < 0.0001$).

Table 13. Location, age and date of trans-Atlantic band recoveries of Northern Gannets (*Morus bassanus*) banded at North American colonies (see Figure 22).

Colony	Band number	Banding date	Recovery age	Recovery date	Recovery location
Funk Is.	0638-73740[1]	Aug 1984	Adult[2]	May 1991	Iceland
	0748-54713	Aug 1988	Adult[3]	Feb 1994	Iceland
	0748-54848[1]	Aug 1988	Adult[4]	Nov 1988	Morocco
	0638-73634[1]	Aug 1984	Immature	Mar 1988	Ireland
	0678-27286	Aug 1979	Immature	Nov 1979	Portugal
	0638-73693[1]	Aug 1984	Immature	Nov 1984	Portugal
	0678-27313[1]	Aug 1979	Immature	Oct 1979	Madeira
	0748-05814	Aug 1986	Immature	Sept 1986	Morocco
Bonaventure Is.	0508-00379[1]	Sep 1967	Immature	Nov 1970	Spain

[1] Details reported in Gaston et al. (2008)
[2] Banded as an immature.
[3] Banding age: "after hatch year".
[4] Banded as an adult.

The rate of trans-Atlantic recoveries differed between Bonaventure Island and colonies in Newfoundland (Funk Island, Cape St. Mary's and Baccalieu Island). Trans-

Atlantic birds accounted for 7.2 % (8 of 111) of the band recoveries from Newfoundland colonies (adults and immatures combined), which was significantly greater than the 0.1 % (1 of 714) of the Bonaventure Island recoveries (Table 14, Fisher exact test, $p < 0.0001$). Considering only adults, trans-Atlantic recoveries accounted for 6.1 % (3 of 49) of Newfoundland recoveries compared to 0 of the 265 recoveries from Bonaventure Island (Fisher exact test, $p = 0.004$).

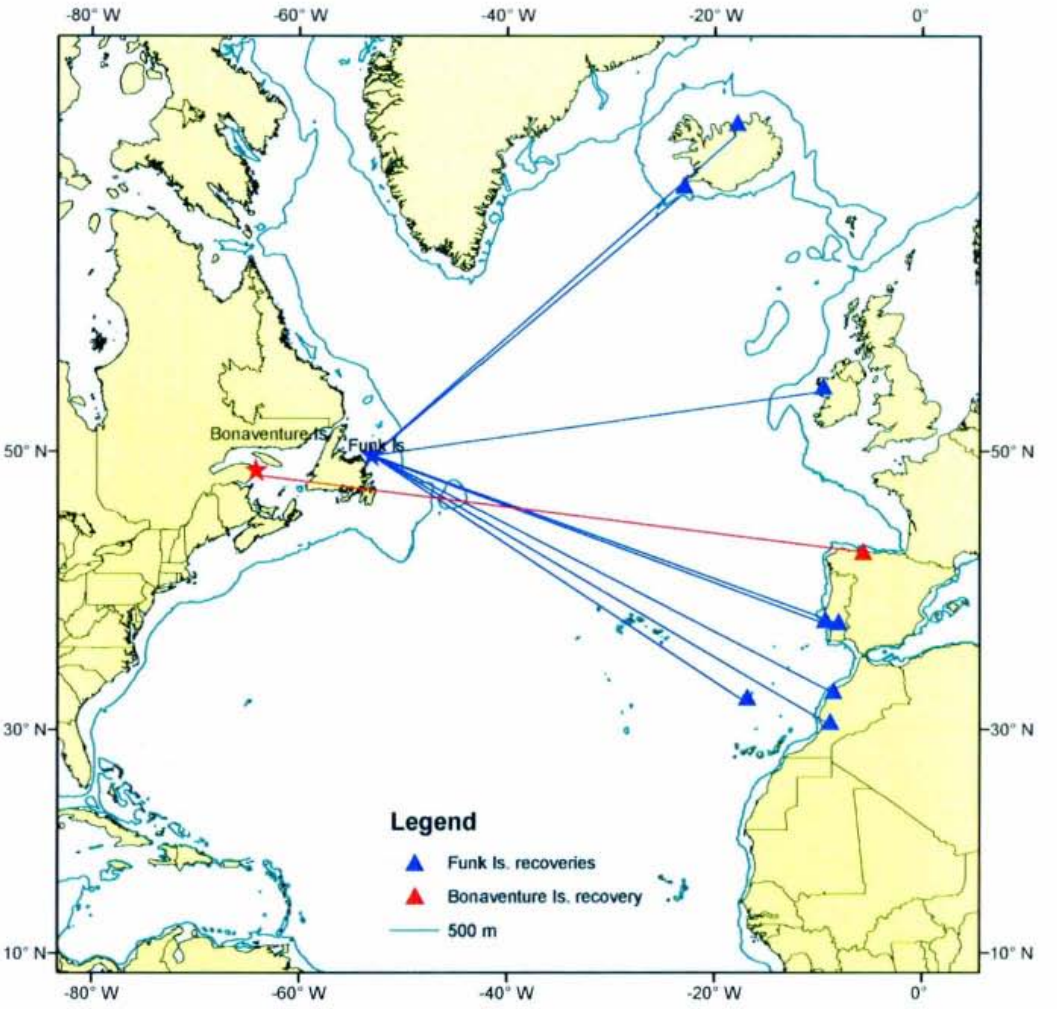

Figure 22. Banding and recovery locations of Northern Gannets (*Morus bassanus*) banded in North America and recovered in the eastern Atlantic Ocean. See Table 13 for details (based on Gaston et al. 2008).

3.3.2 Geolocators

Winter area. Remarkably, three geolocator-equipped gannets (n = 4 trips), one from each of the Newfoundland colonies, displayed a radically different migration and over-winter strategy than those wintering in North America. These birds, one from Cape St. Mary's (80182, sex unknown, hereafter bird "C"), one from Funk Island (80185, female, hereafter bird "F") and one from Baccalieu Island (16295, sex unknown, hereafter bird "B"), undertook previously undescribed round-trip trans-Atlantic migrations to the west coast of Africa (Figure 23, Table 14). The birds spent the winter over the narrow continental shelf along the coasts of Western Sahara, Mauritania and Senegal in the Canary Current. Winter centroids were 4,267, 4,343 and 4,320 km from their respective breeding colonies exceeding the distances of all birds wintering in North America. Interestingly, bird F was tracked again during the following year when it again wintered off the coast of West Africa where its winter centroid was 4,335 km from the colony (the other two birds were not tracked again). Home and core range sizes (home: 171,200 – 309,800 km^2, core: 38,000 – 57,800 km^2) were on the low end of the range sizes for their North American wintering counterparts (Table 15, Figure 9).

The frequency of the two migration strategies (domestic versus trans-Atlantic) in geolocator-equipped birds also differed among North American colonies. Three of 18 breeding gannets from Newfoundland colonies made round trip trans-Atlantic migrations, whereas none of the 28 birds from Bonaventure Island did so (Table 14). This difference in the frequencies, although constrained by limited sample size, approached significance (Fisher exact test, $p = 0.07$).

Table 14. Comparison of domestic and trans-Atlantic Northern Gannet (*Morus bassanus*) band recoveries and round-trip migrations based on geolocators, summarized by colony, region, continent and age.

		Bands						Geolocators		
		Recoveries			Trans-Atlantic recoveries			Over-winter area		
Location	Banded	Adult	Immature	All ages	Immature	Adult	All ages	Domestic	Trans-Atlantic	All
North America										
Newfoundland										
Funk Island	2,853	46	60	106	5	3	8	8	1	9
Cape St. Mary's	42	1	0	1	0	0	0	3	1	4
Baccalieu Island	27	2	2	4	0	0	0	4	1	5
Newfoundland total	2,922	49	62	111	5	3	8	15	3	18
Gulf of St. Lawrence										
Bonaventure Island	10,465	265	449	714	1	0	1	28	0	28
Other[1]	107	1	6	7	0	0	0	-	-	-
North American Total	13,494	315	517	832	6	3	9	43	3	46
Europe										
Bass Rock, Scotland								22	0	22
European Total	62,328	-	-	3,218	0	0	0	22	0	22

[1] Gannets banded along the east coast of North American, colony of origin unknown.

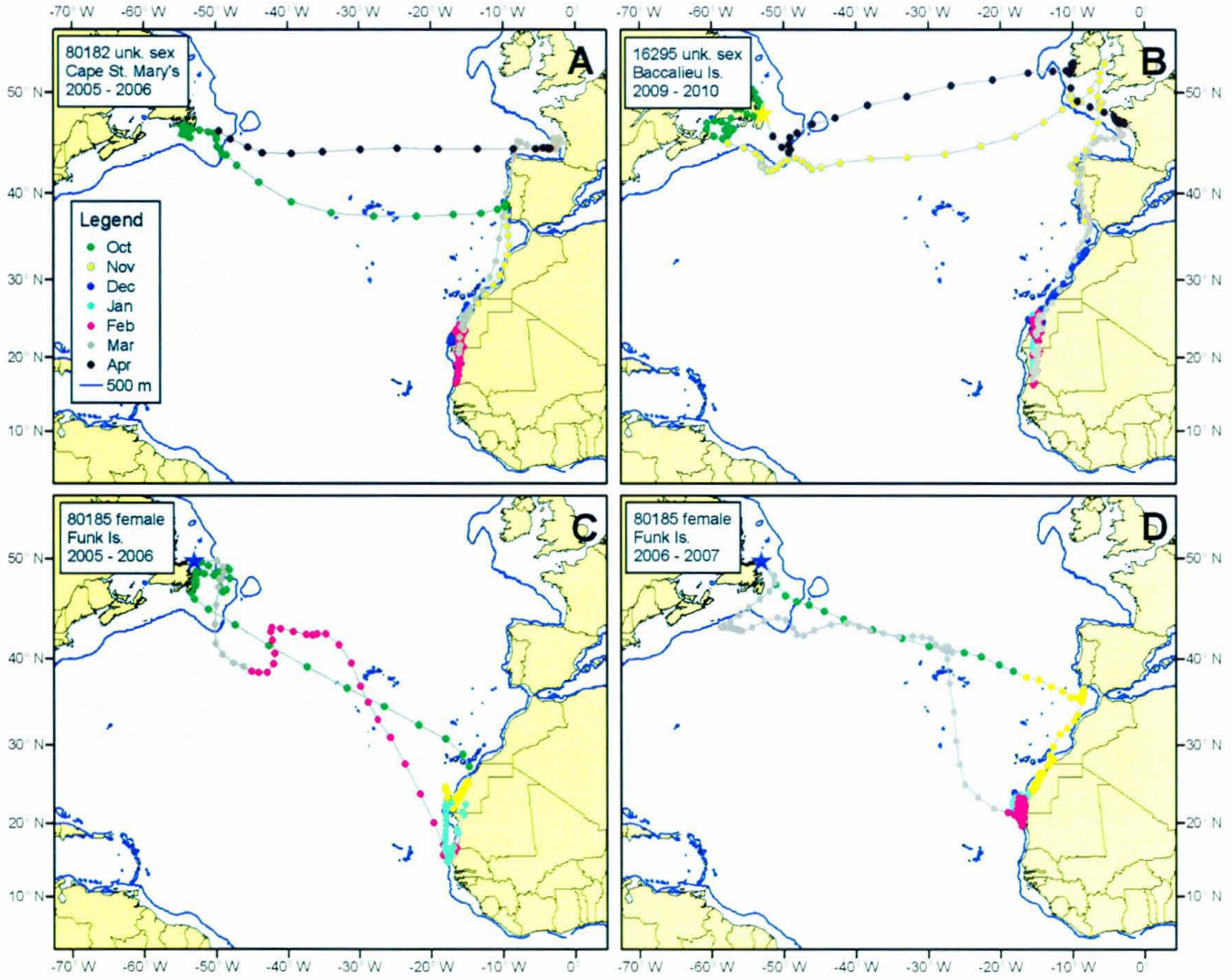
80182 unk. sex
Cape St. Mary's
2005 - 2006
A
Legend
Oct
Nov
Dec
Jan
Feb
Mar
Apr
500 m
16295 unk. sex
Baccalieu Is.
2009 - 2010
B
80185 female
Funk Is.
2005 - 2006
C
80185 female
Funk Is.
2006 - 2007
D
-70° W
-60° W
-50° W
-40° W
-30° W
-20° W
-10° W
0°
50° N
40° N
30° N
20° N
10° N

Figure 23. Tracks of trans-Atlantic migration and wintering on the coast of western Africa by three Northern Gannets (*Morus bassanus*) breeding at (A) Cape St. Mary's (2005-06), (B) Baccalieu Island (2009-10), (C) Funk Island (2005-06) and (D) the same bird from Funk Island in 2006-07. Dots represent bird positions (two per day).

Table 15. Migration parameters and winter range sizes of North American breeding Northern Gannets (*Morus bassanus*) wintering on the west African coast.

	Bird C Cape St. Mary's 2005-06	Bird F Funk Island 2005-06	Bird F Funk Island 2006-07	Bird B Baccalieu Island 2009-10
Fall				
Start date	6 Oct	15 Oct	24 Oct	17 Oct
Begin Atlantic crossing	26 Oct	27 Oct	26 Oct	8 Nov
End Atlantic crossing	30 Oct	1 Nov	3 Nov	15 Nov
Duration Atlantic crossing	5	4	9	7
Distance Atlantic crossing	3,586	3,810	3,502	3,322
Speed Atlantic crossing (km d^{-1})	717	762	389	475
Stopover Atlantic crossing	0	0	0	0
End date	6 Nov	5 Nov	16 Nov	9 Dec
Duration (d)	31	22	23	54
Stopovers (d)	14	6	2	17
Distance (km)	6,343	6,347	5,899	10,145
Speed (km d^{-1})	205	289	256	188
Winter				
Home range size (km^2)	171,200	226,000	213,600	309,800
Core range size (km^2)	38,000	39,700	57,500	48,300
Days in winter area	127	104	105	94
Spring				
Start date	13 Mar	17 Feb	1 Mar	14 Mar
Begin Atlantic crossing	4 Apr	17 Feb	1 Mar	9 Apr
End Atlantic crossing	8 Apr	03 Mar	16 Mar	13 Apr
Duration Atlantic crossing	5	15	16	4.5
Distance Atlantic crossing	3,397	5,409	4,587	2,758
Speed Atlantic crossing (km d^{-1})	679	361	287	613
Stopover Atlantic crossing	0	0	0	4
End date	9 Apr	7 Mar	29 Mar	17 Apr
Duration (d)	28	18	28	34
Stopovers (d)	9	3	10	12
Distance (km)	7,435	6,016	6,392	7,584
Speed (km d^{-1})	266	334	229	223

Migration. In 2005, bird C and bird F departed their colonies (separated by 350 km) nine days apart in October and remained on the Grand Bank until the last week of October. They then departed Canadian shelf waters within a day of one another on 26 – 27 October (Figure 23). Unfavourable northeast headwinds dominated the days leading up to 26 October 2005, when a low-pressure system moving up the eastern North American coast began to generate favourable tailwinds. Over the next 5 days, both birds essentially rode this low-pressure system across the North Atlantic traveling distances of *ca.* 3,600 to 3,800 km with tail winds of up to 60 km h^{-1} (Figure 24). Bird C took a northerly route reaching coastal Spain travelling at a speed of 717 km d^{-1} and then within a few days moved south to arrive at its wintering area off Western Sahara by 6 November (Figure 23A). Bird F took a more direct route *via* Canary Islands averaging 762 km d^{-1} to reach the coast of Western Sahara by 1 November 2005 where it stopped until early January before moving south to spend the rest of the winter off coast of Senegal (Figure 23C).

Timing and routes of return spring migration differed between these two birds. In mid-March 2006, bird C retraced its route northward spending late March in the Bay of Biscay, and on 4 April it departed, moving westward between a low pressure system to the south and a weaker high pressure system to the north (Figure 25). Its route took it up to 800 km north of its eastward autumn crossing (Figure 23), re-crossing the North Atlantic in 5 days using tailwinds of 18 – 43 km h^{-1}, at a speed of 679 km d^{-1} to arrive on the Canadian shelf by 8 April 2006. In contrast, bird F initiated its return much earlier on 17 February 2006. It made good progress for the first five days but, encountered strong

cross and headwinds of 40 – 60 km hr^{-1} in the central Atlantic from a low pressure system stalled over Newfoundland (Figure 26). It then progressed slowly for the next 9 days on a more circuitous route to reach Canadian shelf waters on 3 March 2006. Overall, it covered 5,409 km on its 15 day crossing, averaging only 361 km d^{-1} during its crossing.

In 2006-07, bird F departed the colony on 24 October and departed Canadian shelf waters on 26 October, one day earlier than the previous year (Figure 23D). It took a more northerly route than in 2005, using tailwinds of 35 – 70 km hr^{-1}, to reach coastal waters off southwestern Portugal after covering 3,502 km in nine days at a speed of 389 km d^{-1}, about half its speed in the previous year. It then proceeded south along the African coast to reach its winter area by 16 November. Remarkably, it remained on the winter grounds only one day longer than in the previous year. Its return migration, beginning on 1 March 2007, was the longest of any trans-Atlantic trip (16 days) and the only one to feature a stopover. After leaving the African coast, it proceeded almost due north in head, tail and cross winds of *ca.* 25 km hr^{-1} until intersecting its fall route north of the Azores, where it paused for 4 days. During its stopover, south-westerly, westerly and north-westerly headwinds of 15 – 35 km h^{-1} predominated. On 10 March 2007, it departed the stopover area with a 50 km hr^{-1} south-westerly tail/cross wind. For the final 9 days of the journey it experienced variable head- and crosswinds of 15 – 50 km h^{-1} before reaching the Canadian shelf by 13 April covering 4,587 km across the Atlantic at an overall speed of 229 km d^{-1} for the entire trip.

In comparison to the first year, Bird F spent part of the winter further north and did not venture south to the Senegal coast in the second year. This contributed to its fairly

large distance between winter centroids of 295 km. Likewise, core ranges did not overlap at all and home range overlaps were relatively low (year 1 on year 2: 21 %, year 2 on year 1: 22 %).

The final trans-Atlantic bird, bird B, departed Canadian shelf waters on 8 November 2009 (Figure 23B) following a similar (though more northerly) fall migration route as Bird C to reach the continental shelf waters of the Celtic Sea in seven days. It experienced tailwinds of 25 – 60 km h^{-1} throughout the crossing, covering 3,322 km at a speed of 475 km d^{-1}. Upon arrival in European waters, it made a brief sojourn to the Irish Sea, bringing it near the colonies at Great Saltee and Grasholm, before following the coast south to reach its winter area by 9 December. In spring, it retraced its route north making brief stops in the Bay of Biscay and off the southwest coast of Ireland near the colonies at Little Skellig and Bull Rock. After several days of westerly head winds, it departed the Irish coast on 9 April with a 40 km h^{-1} tail/cross wind. It re-crossed the North Atlantic via a direct route covering 2,758 km in just 4.5 days at a speed of 613 km d^{-1}. It reached the Canadian shelf on 13 April having enjoyed strong tail/cross winds of 30 – 50 km h^{-1} for the first 3 days and variable/head winds of 20 km h^{-1} thereafter.

The dates of colony departure for trans-Atlantic migrants were within the range of those for domestic wintering birds from the same colony in the same year. Bird C was the only bird tracked from Cape St. Mary's in 2005-06 and had a departure date that was 3 days earlier than other Newfoundland (i.e. Funk Island) gannets. Colony arrival dates for birds B and C were within the range of arrival dates for other domestic wintering birds at the same colony (Bird B) or in same region (i.e. Newfoundland, Bird C) in the same year.

However, bird F arrived 29 days earlier than any other Funk Island bird in 2006 and 23 days earlier in 2007. Migration distances (fall: 5,899 – 10,145 km, spring: 6,016 – 7,584 km), durations (fall: 23 – 54 d, spring: 18 – 34 d) and number of stopover days (fall: 2 – 17 d, spring: 3 – 12 d) were similar to those of birds wintering in the Gulf of Mexico and for North American migrants in general. The overall speed of fall (188 – 2289 km d^{-1}) and spring (223 – 334 km d^{-1}) migrations, including both trans-Atlantic and coastal shelf portions, were on the high end of those of their domestic wintering conspecifics (fall: 71 – 184 km d^{-1}, spring: 84 – 486 km d^{-1}) owing to the exceptionally swift (in most cases) trans-Atlantic crossings. In comparison to fall, spring migration duration was shorter, speed was faster, and the number of stopover days was fewer for all migrations except for Bird F's repeat migration of 2006-2007, which was characterized by a slow return with stops in the central Atlantic and eastern Scotian Shelf (Figure 23D).

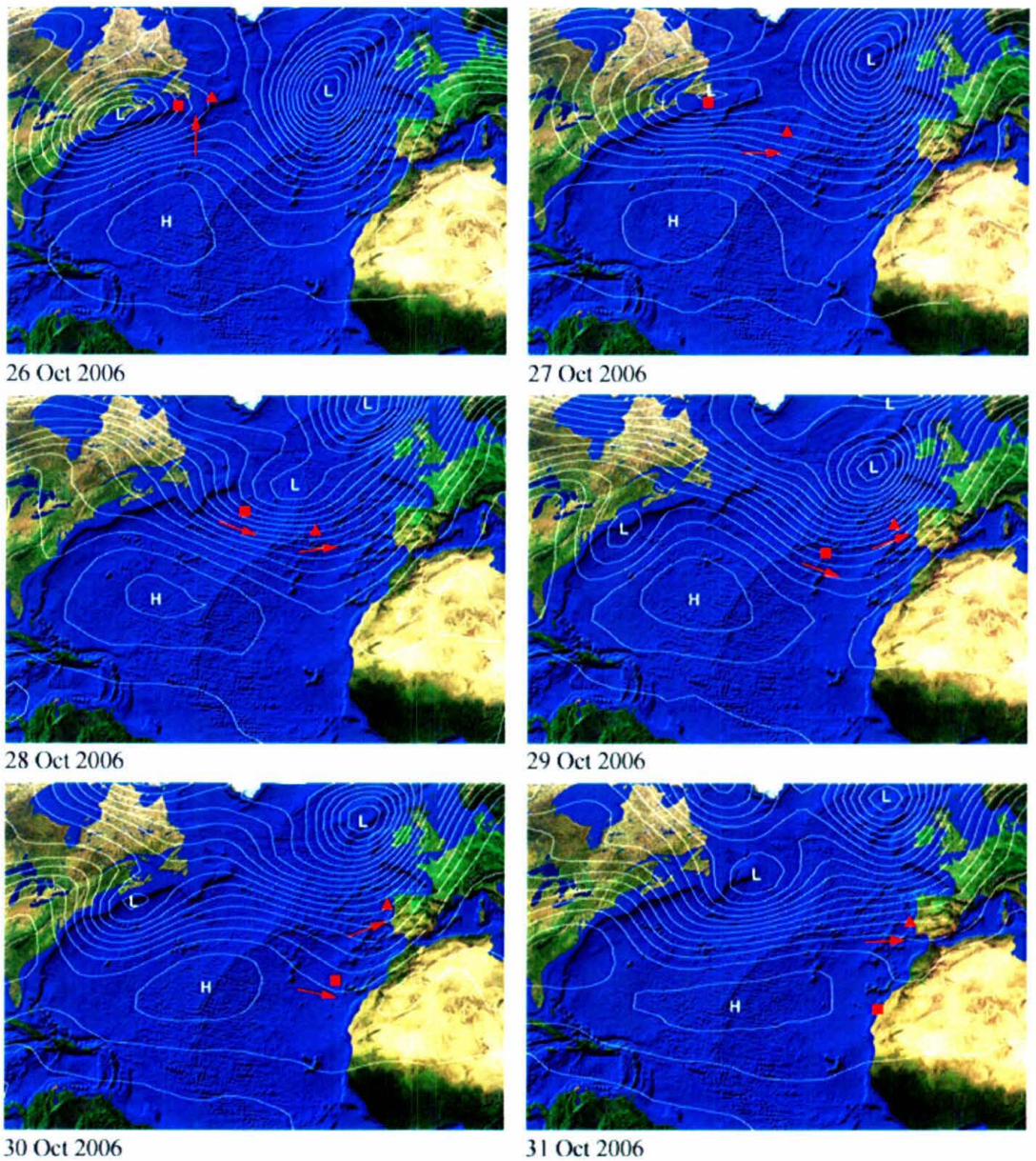

Figure 24. Wind patterns (red arrows) assisting eastward fall trans-Atlantic migrations of Northern Gannets (*Morus bassanus*) from Funk Island (squares) and Cape St. Mary's (triangles). Arrow length is proportional to wind speed.

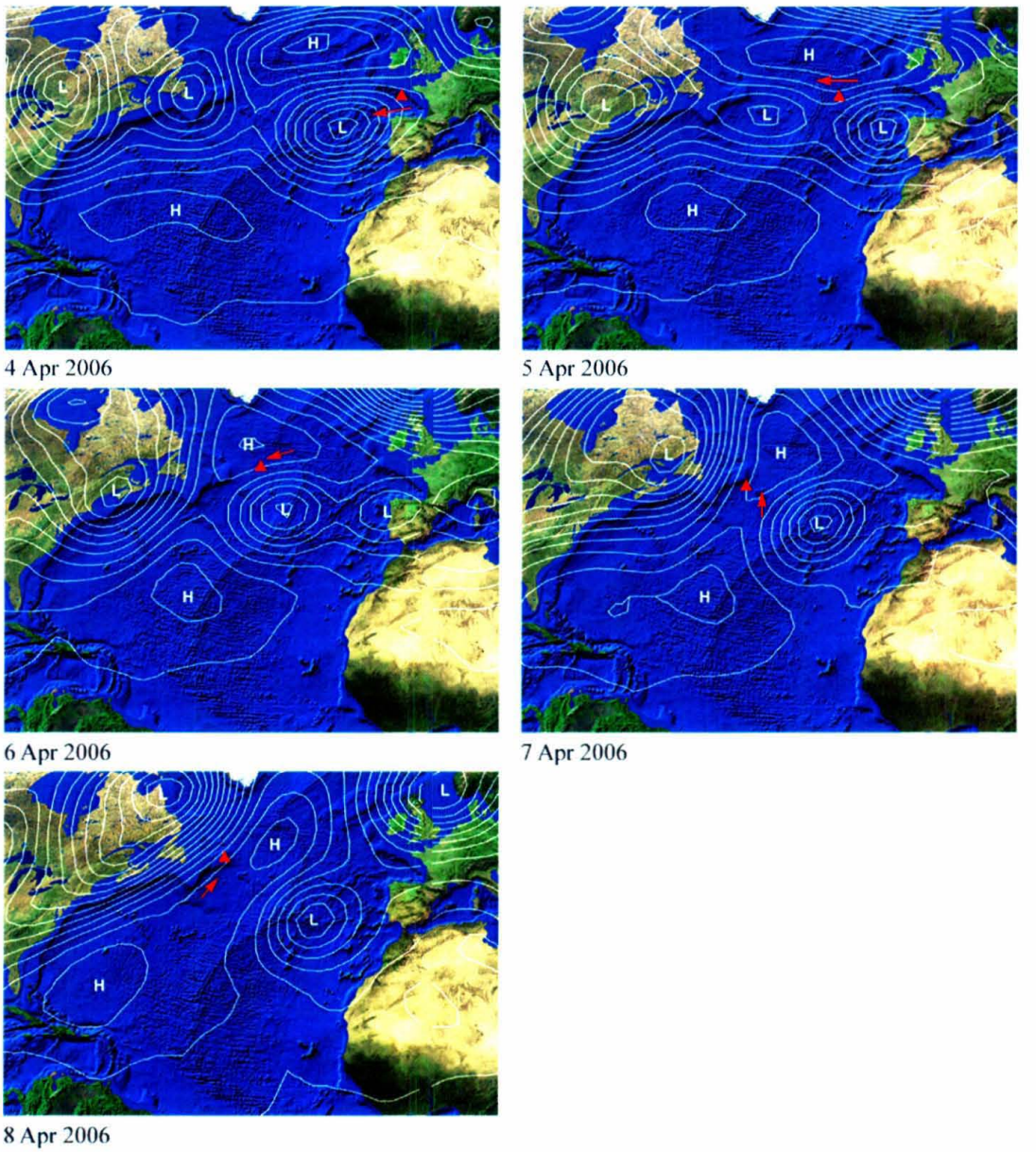

Figure 25. Wind patterns (red arrows) affecting westward spring trans-Atlantic migration of a Northern Gannet (*Morus bassanus*) breeding at Cape St. Mary's showing initial wind assistance on the first two days. Red triangles show bird position, arrow length is proportional to wind speed.

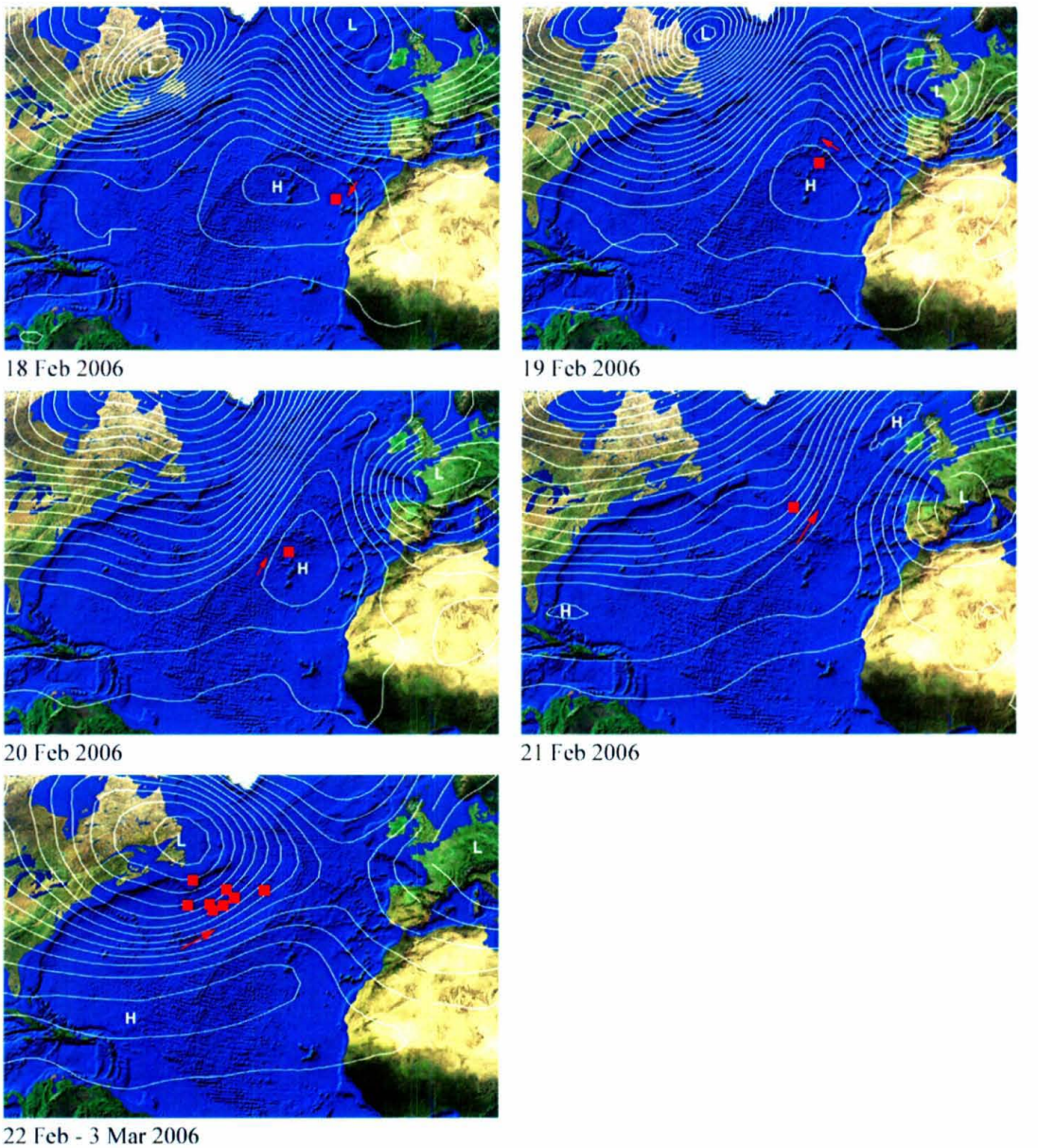

Figure 26. Wind patterns (red arrows) affecting westward spring trans-Atlantic migration (red squares) of a Northern Gannet (*Morus bassanus*) breeding at Funk Island. Red triangles show bird position, arrow length is proportional to wind speed. Final panel is a composite of 22 Feb - 3 Mar 2006, influenced by a stalled low pressure system.

3.4 Integration of bands and geolocators

Both bands (all non-breeding) and geolocators indicated that *ca.* 60 % of gannets wintered in the northeast zone in North America, but the proportions in the other zones differed (Fisher exact test, $p = 0.016$; Table 2; Table 4). About one-third of band recoveries occurred in the southeast compared to only 10 % of geolocator-equipped birds with centroids in this zone. Only 6 % of adult band recoveries versus 28 % of geolocator-equipped wintering birds occurred in the Gulf of Mexico. Similar patterns were evident when Bonaventure Island and Funk Island were examined individually, but band recovery sample sizes were low and the differences could not be established statistically (Bonaventure Island: Fisher exact test, $p = 0.18$; Funk Island: Fisher exact test, $p = 0.10$; Table 2; Table 4). Further, the tendency for Funk Island geolocator-equipped gannets to remain further north within the northeast zone than Bonaventure Island birds was not apparent in band recoveries. Since only a single band recovery came from a known-sex bird, no meaningful sex comparison could be made between bands and geolocators. Both technologies indicated trans-Atlantic crossing, although only geolocators clearly showed *round-trip* migrations. In concurrence with banding results, the proportions of trans-Atlantic crossing birds was higher for Newfoundland colonies than for Bonaventure Island.

Speeds of gannet migration (fall: 24 – 32 km d^{-1}, spring: 56 – 112 km d^{-1}) ascertained by bands (Gaston et al. 2008) were considerably slower than the speeds indicated by geolocators (fall: 110 ± 20 km d^{-1}, spring: 164 ± 72 km d^{-1}).

4 Discussion

Device Effects. Gannets are the largest seabird in the North Atlantic and the tiny geolocator devices likely did not cause significant negative effects. Body mass did not differ before deployments and after return and recapture. Return rates for equipped gannets were comparable to gannet survival (Nelson 2002; Mowbray 2002). No ill effects were found when gannets carried these (Kubetzki et al. 2009), and larger and heavier devices (Garthe et al. 2007a, 2007b; Lewis et al. 2002). Further, no significant effects were found for similar size loggers on much smaller Cory's Shearwaters (Igual et al. 2008).

4.1 North American winter areas - distribution, connectivity and scale

At the global scale, gannets displayed strong connectivity with the majority of North American breeders wintering domestically. Yet, three individuals, one from each Newfoundland colony, displayed a radically different strategy and crossed the Atlantic Ocean to winter on the coast of Africa. At the continental level, the gannet population as a whole displayed weak to moderate connectivity by wintering across a broad geographic range in North America while favouring a number of distinct winter zones and hotspots. Most individuals did not wander widely, but instead remained within relatively small, discrete winter ranges. Range sizes did not differ between sexes or destination, and the difference in range size between Bonaventure Island and Funk Island in 2005-06 was an artefact of extremely large ranges for two birds from Bonaventure Island and probably

does not represent an ecological difference in the winter ranges of gannets from these two colonies.

Range sizes were smaller for Funk Island birds in 2005-06 in comparison to 2006-07. This could be an artefact of the small Funk Island sample sizes but several pieces of evidence suggest that conditions in 2006-07 required larger home ranges, perhaps due to prey availability, than in 2005-06. Firstly, 5 of the 6 gannets tracked to North American wintering areas from Funk Island in 2006-07 were the same birds tracked from this colony during 2005-06 (n = 8), thus the change in range sizes was not an artefact of sampling different birds in different years. Secondly, range sizes for the small number of birds tracked from Cape St. Mary's in 2006-07 were similar to those for Funk Island suggesting that this was the norm for 2006-07 and not just a result specific to Funk Island gannets. Thirdly, range sizes were similar in 2005-06 between Funk Island gannets and the larger sample of birds at Bonaventure Island (ignoring the two outliers), and range sizes at Bonaventure Island were similar between 2004-05 and 2005-06. Taken together, these facts indicate that 2006-07 was anomalous compared to previous years. There was, however, considerable individual variation implying some measure of flexibility for this trait. Likewise, gannets breeding at Bass Rock, Scotland showed considerable individual variation and consistent range size between wintering areas (Kubetzki et al. 2009). Gannets wintered across a broad latitudinal range in North America and concentrated in regions that were typified by widely divergent thermal regimes, indicating a lack of habitat specialization. Similarly, Australasian Gannets wintered at a variety of locations in Australian and Tasmanian coastal waters (Ismar et al. 2011).

The hotpots in the Gulf of Maine, from Long Island to Chesapeake Bay, and in the Gulf of Mexico may reflect the distribution of prey. Although little detailed information exists regarding gannet winter diet, in North America they are known to forage on a variety of schooling fish that includes menhaden (*Brevoortia* spp.; Mowbray 2002). Similar to capelin (*Mallotus villosus*), which are consumed during the breeding season (Montevecchi et al. 2009), menhaden support a diverse food web of piscivorous fish, seabirds and marine mammals (Franklin 2007; Carscadden and Nakashima 1997). Like the capelin, menhaden exhibit a complex cycle of population fluctuations and are the target of the second largest commercial fishery (by weight) in the United States (Pritchard 2008). On the Atlantic coast, large stocks of menhaden previously occurred in the Gulf of Maine but were over-fished for the reduction industry (Franklin 2007). Nonetheless, industrially fished stocks still occur along the mid-Atlantic coast from Cape Cod to Cape Hatteras. This area is also a winter hotspot for bluefin tuna whose main prey is menhaden (Wilson et al. 2005). The largest remaining menhaden stocks in the northern Gulf of Mexico are the target of the largest and most recently developed industrial fishery (Vaughan et al. 2007; Franklin 2007). Gannets (and their congeners) are attracted to pelagic forage fish and also to discards from fisheries (Montevecchi et al. 2009; Käkelä et al. 2007; Pichegru et al. 2007; Garthe et al. 2007a). Thus, the increase in gannets in the Gulf of Mexico could result from a combination of a relative decline in menhaden stocks on the Atlantic coast in comparison to the Gulf of Mexico and increased fish discards in the Gulf (Franklin 2007). In this case, the observed weak connectivity in North American winter distribution could simply be in proportion to available resources, essentially an

ideal free distribution on a large-scale (Fretwell and Lucas 1970). Geolocator-equipped gannets breeding at Bass Rock, Scotland wintered in one of four distinct areas and a similar southerly shift in distribution toward the west African coast (relative to banding records) was associated with both the availability of pelagic fish in a highly productive upwelling system (Wynn and Knefelkamp 2004) and discards from intensely prosecuted fisheries that have increased during recent decades (Camphuysen and van der Meer 2005). Likewise, recent distributional shifts in Cape Gannets breeding in Africa have been associated with changes in prey distribution and fishing effort (Pichegru et al. 2009; Crawford et al. 2007). Similarly, White-chinned Petrels wintered in discrete regions with differing depths and thermal characteristics, with the relative abundance of prey determining distribution (Phillips et al. 2006). The availability of prey most likely had a strong influence on determining gannet distribution and the within-year fidelity to such small discrete core areas (that could be crossed in a few hours flight in most cases) implies the existence of predictable prey at this scale. Studies focused on winter diets employing tracking, intrinsic markers (e.g. stable isotopes and fatty acid signatures), and habitat selection in relation to food availability (Wakefield et al. 2009) could help to further elucidate the mechanisms responsible for changes in gannet distribution on both sides of the Atlantic Ocean (Kubetzki et al. 2009).

A number of gannets that wintered in the northeast (southeast) zone also made excursions into the neighbouring southeast (northeast) zone to varying extents, with one bird having a winter range that covered most of the northeast zone in one year and all of the northeast and southeast sectors combined in the next. However, no bird in either the

northeast zone or southeast zones ventured into Gulf of Mexico (or vice versa), indicating that the choice between the north- and southeast may be more plastic than the choice between these areas and the Gulf of Mexico or that longer distance migrants have more discrete target areas.

The previously published contention that the Florida coast is the main wintering area for gannets in North America (Nelson 2002) was not substantiated by band or geolocator analyses. This former conclusion was based on band returns of all ages combined, whereas the adult band returns analyzed here indicated roughly equal importance of the northeast and southeast zones. Further, only seven migrations by five individuals terminated in the southeast sector implying that it is a less desirable destination. Yet, this zone had the greatest number of year-round band returns, mostly from immature birds (Gaston et al. 2008; Nelson 2002). It may be that this area is favoured by immature birds (from which most recoveries come), thus biasing the comparison. High proportions of immature and juvenile gannets occur in the Gulf of Mexico (Nelson 2002), so some of these birds in southeast may have been in transit; immatures, especially juveniles also experience high mortality especially during their first migrations. This area also has a large amount of human-frequented beach habitat where carcasses deposited by (perhaps relatively more onshore) currents are more likely to be detected than in other areas. Alternatively, the large number of band returns (primarily from dead gannets) and the low number of geolocator-equipped birds wintering in the southeast could indicate that this is a poor quality area. Indeed, several mass die-offs of gannets and other species have occurred in the southeast zone in recent

decades (Lee 2009; B. Monk, pers. comm.). Likewise, male Great Cormorants wintering at intermediate distances had lower fitness than those wintering closer to or farther from the colony and a similar (unexplained) mechanism could also be responsible for the paucity of gannets wintering in the southeast zone.

Most geolocator-equipped birds wintered in the northeast zone, remaining relatively close to the breeding grounds. This preponderance of birds in the northeast zone might indicate that birds choose to go only as far as necessary to find adequate resources for winter survival (Gauthreaux 1982) and that most achieved this by staying in the northeast. The large proportion of adult geolocator-equipped gannets wintering in the Gulf of Mexico was also unexpected, since band recoveries indicated that a very small proportion of the adult population wintered there. These differences could be indicative of biases in band recoveries, and recovered birds in the northeast and southeast could have been in transit to or from other regions. Alternatively, this may herald a recent shift in winter distribution, since there was a lack of temporal overlap (by decades) between band returns (1930s – 1990s) and geolocators (2004 – 2010). Small winter ranges make gannets vulnerable to mortality from regional or localized events and the extent of the oil from the 2010 *Deepwater Horizon* spill in the Gulf of Mexico overlapped all or part of the home range of most geolocator-equipped birds wintering there. Increasing numbers of adult gannets wintering in the Gulf of Mexico raises considerable concern for direct and indirect mortality from the on-going effects of this spill (Montevecchi et al. 2011).

4.1.1 Colony comparison

When comparing colonies, it is difficult to draw firm conclusions from the band recovery results due to low samples sizes, especially for Funk Island recoveries during winter. However, banded birds appeared to display a lack of population structuring. Recoveries from Funk Island and Bonaventure Island occurred in all three zones during both non-breeding and winter, with the exception of an absence of Funk Island recoveries in the Gulf of Mexico during winter. Geolocator evidence indicates slightly stronger population structuring. The four breeding populations (Bonaventure Island, Funk Island, Cape St. Mary's, Baccalieu Island) overlapped during winter in North America to a large extent. Yet, birds from Newfoundland colonies wintered only in the nearest (northeast) and the most distant (Gulf of Mexico) zones, avoiding the southeast. This result is at odds with the adult banding data, possibly indicating that the adult Funk Island winter band recoveries in the southeast zone were from birds in transit to/from the Gulf of Mexico. Alternatively, the lack of Newfoundland geolocator-tracked gannets wintering in the southeast zone may simply be due to small sample size.

In the northeast zone, Funk Island gannets (from colder water environments) tended to winter further north within the zone than those from Bonaventure Island, however winter ranges for Baccalieu Island gannets overlapped those from Bonaventure Island. These distribution patterns indicate some degree of winter habitat partitioning between populations. The observed distribution is, however, limited by the small sample size of both bands and geolocators from Newfoundland gannets. Similarly, Cory's Shearwaters from three breeding populations showed preferences among wintering areas

while exhibiting considerable overlap among populations (González-Solís et al. 2007). African Cape Gannets breeding and foraging in two distinct upwelling systems wintered in different areas but, unlike Northern Gannets, they did not undertake long-range migrations, instead remaining in the same habitat year-round (Jaquemet and McQuaid 2008). Several other species of procellariiforms use multiple distinct wintering areas (e.g. Yamamoto et al. 2010; Hatch et al. 2010; Phillips et al. 2008, 2006, 2005; Shaffer et al. 2006; Croxall et al. 2005; Weimerskirch and Wilson 2000), but most studies have focused on single colonies, so few data are available with which to compare population structuring during winter.

4.1.2 Sex comparison

Intriguingly, almost two-thirds (64 %) of known-sex birds that were equipped with geolocators were males. Bird captures occurred at several locations within each colony and at varying times during the day. This suggests that males spend more time chick guarding than females during the day (when there is more aggression and disturbance at the nest-site) although females are reported to have significantly longer brooding shifts (Mowbray 2002). Alternatively, if a pair was in attendance when investigators attempted captures, the less aggressive females may have departed (which seemed to be the case in a few instances in the field), biasing the sex ratio of the sample. Nonetheless, contrary to prediction, there was no evidence of males wintering closer to the breeding colonies than females. The winter ranges of male and female geolocator-equipped birds overlapped completely. Only one band recovery included sex, so this shed no further light. Differential distance migration, in order to evolve, normally requires a

higher cost for migrating further and an isolating mechanism between the sexes. Three main hypotheses have been developed to account for the isolating mechanism: differential cold-weather resistance due to sexual dimorphism allowing one sex to winter farther north (body size hypothesis), competitive exclusion due to social dominance (dominance hypothesis), and pressure for one sex to arrive at the breeding areas earlier (arrival time hypothesis; Cristol et al. 1999). Gannets are sexually monomorphic and are likely equally suited to survive winter conditions throughout their range. Also, there is no evidence of a sex-bias in interference competition in gannets (Lewis et al. 2002) such as in, for example, Giant Petrels (*Macronetes* spp.) where males exclude females at carrion (González-Solís et al. 2008). Male gannets are reported to arrive earlier at the colony than females in order to defend nest sites (Nelson 2005). If this is true, it is not due to wintering closer as predicted by the arrival time hypothesis. Instead, males would simply need to leave winter areas before females or travel faster to arrive earlier at the colony. This also did not occur (see section 4.2.1). There may also be little incremental cost for migrating long distances along a productive continental shelf, precluding selection for differential migration. However, female gannets from Bass Rock, Scotland wintered further from the breeding colony on average, although the difference was not statistically significant (Kubetzki et al. 2009). Several large sexually dimorphic albatrosses and Giant Petrels showed weak differences in non-breeding season $\delta^{13}C$ (but not in $\delta^{15}N$), indicating differences in distribution (likely due to niche specialization), but a lack of dominance exclusion, leading to similar trophic levels (Phillips et al. 2009). It is possible that gannets did display fine-scale spatial segregation and/or niche specialization. More

accurate tracking methods and/or biochemical assays of gannet feathers grown during winter are needed to address this question at a fine scale (Furness et al. 2006).

4.1.3 Winter site fidelity

This is one of only two studies to report winter site fidelity in a non-procellariiform pelagic seabird (Frederiksen et al. 2002). On a global scale, all birds wintered on the same side of the Atlantic Ocean in successive years while, on a regional scale, all birds returned to the same oceanographic zone and had median inter-centroid distances of only 87 km between years. There was also considerable overlap at the scale of individual ranges. Most home ranges had overlap indices exceeding 50 % and core ranges overlapped by more than 30 % (Figure 13). These findings indicate a remarkable tendency to return to a spatially restricted area in consecutive years. For many species, fidelity to the breeding area is markedly greater than that to the winter grounds, whereas in other species the opposite is true. Like most colonial seabirds, gannets are highly philopatric to their breeding colony and to an individual nest site. This behaviour (and indeed the location of colonies) has evolved to take advantage of predictable prey aggregations within foraging range during the breeding season. Likewise, winter-site fidelity on the scale observed in this study has likely evolved to take advantage of spatially predictable seasonally variable prey and habitat (Mueller and Fagan 2008). Gannets exhibited colony-based differences in fidelity to distinct foraging areas during the breeding season that were mediated by differing prey predictability within foraging range of the colony (Garthe et al. 2007b; Hamer et al. 2001). No colony-based differences in winter site fidelity rates were found in this study, likely because birds from

different colonies overlapped in their wintering areas to some extent or because prey availability did not differ substantially between areas. Likewise, no sex-based differences in winter site fidelity were observed, although these findings are not surprising given the small number (n = 16) of consecutively tracked birds.

Winter site fidelity has only been reported for a small number of seabird species. Surprisingly, winter site fidelity in the Wandering Albatross was established by repeat sighting of banded birds (Weimerskirch and Wilson 2000) on their wintering grounds. Cory's Shearwaters had inter-centroid distances of (1,901 ± 2,886 km) in repeat years that differed significantly from that expected by chance (Dias et al. 2010). Repeat-year inter-centroid distances of gannets were also significantly closer together than expected by chance and were more than an order of magnitude closer together than those of the shearwaters. Gray-headed Albatrosses showed consistency in choice of staging areas and in timing and routes of circumnavigations (Croxall et al. 2005) while a single White-chinned Petrel tracked in successive years from South Georgia inhabited the same areas of the Patagonian Shelf and Humboldt Current (Phillips et al. 2006). Twenty-four Black-browed Albatrosses displayed fidelity to widely separated winter areas and exhibited correlated centers of activity within those areas in consecutive years, prompting the authors to suggest fidelity might be common in albatrosses (Phillips et al. 2005). Although some Cory's Shearwaters switched sites between years, others displayed high site fidelity (Dias et al. 2010). Indeed, it may be that winter site fidelity is common in seabirds in general.

At least three hypotheses have been put proposed to explain winter site fidelity. The local knowledge hypothesis posits that return to the same area in subsequent years confers an advantage through knowledge of localized prey resources, predator distribution and behaviour, and location of conspecifics. For a highly mobile apex predator like the gannet, the location of predictable prey may be the most important of these for increased winter survival and body condition that carries over proximately into the next breeding season and ultimately to fitness (Norris and Marra 2007; Furness et al. 2006; Marra et al. 1998). Predictable aggregations of once hyper-abundant prey (e.g. menhaden) in the Gulf of Maine, Chesapeake Bay, and Gulf of Mexico likely influenced the evolution of this trait. The small core (and home) ranges of most gannets imply intensive knowledge of prey distribution, supporting this hypothesis. Two alternative hypotheses explaining winter site fidelity appear less suited to gannets. The genetic hypothesis requires that individuals consistently select a winter site in order to maintain an optimal level of inbreeding (Robertson et al. 2000; Greenwood 1987). This hypothesis is appropriate for waterfowl that pair on their winter grounds but lacks explanatory power for gannets that are not known to do so. Likewise, the social cohesion hypothesis, whereby site fidelity allows family groups to stay together and/or pairs to reunite appears inappropriate for gannets. Juvenile gannets depart their breeding colonies independent of adults and are not known to remain in family groups at sea, and while nothing is known of pair behaviour during winter, the single pair in this study did not winter together. Marine pollution, fishery interactions, and climate change have the potential to bring about substantial changes in prey predictability and habitat quality in a relatively short

timeframe. Gannets exhibit considerable plasticity in prey species and foraging range in response to oceanographic changes at their breeding colonies (Montevecchi et al. 2009; Garthe et al. 2007a) but the ability of gannets to respond through plasticity in winter site fidelity on an appropriate spatial and temporal scale is unknown. In this context, the process whereby an immature gannet eventually settles on a consistent winter site may have long-term implications. Is the location of the winter site inherited? Do juveniles randomly follow groups of conspecifics to a winter site and, having wintered there successfully once, simply return to this familiar territory in successive years (often bypassing perfectly suitable habitat en route)? The resolution of these questions has important implications for gannet (and many other birds) conservation and evolution, and will require synoptic tracking of parents and offspring.

4.2 North American Migration

4.2.1 Colony departure and arrival timing

There was remarkable synchrony in colony departure and arrival timing, with the overall range in each being similar at 26 and 29 days respectively. Even greater synchrony was observed for specific colonies in specific years, with maximum departure and arrival date ranges of only 19 and 18 days respectively. Gannets breeding at Bass Rock, Scotland were slightly more variable in initiating migration, with a range spanning almost one month. To a large extent, the timing of chick fledging, mediated through growth and development, likely determines colony departure date for adults. This is corroborated by the fact that failed breeders and non-breeders typically depart earlier than

breeders (Nelson 2002). But, there is likely little selective pressure for expedient fall departure (up to a point; McNamara et al. 1998). Indeed, some gannets occupied northern waters well into December, indicating that prey is still available and temperatures adequate long after fledging has occurred.

The date of colony arrival was similar to those previously published (Mowbray 2002) for North American colonies and contrary to colonies in the eastern Atlantic, there was no indication of later breeding compared to past decades (Wanless et al. 2008). The benefits of early arrival on the breeding grounds are well known (Drent et al. 2006; Kokko 1999). Early arrival accrues fitness benefits since reproductive success decreases with increasing breeding date in most (Drent et al. 2003) but not all (Phillips et al. 2005) avian species, including gannets (Nelson 2002). But, arriving too early incurs the cost of a mismatch between arrival timing and availability of resources for survival (Bêty et al. 2004). Most birds (including some seabirds; Bond and Diamond 2010) employ a combined capital and income breeding strategy (Drent et al. 2006) and sufficient accumulation of nutrients for egg formation must occur during and/or after migration to the breeding colony. The faster this can be accomplished, the sooner breeding can take place and the higher success will be. Thus, females should aim to arrive as early as possible (but not too early) with excess energy reserves to produce superior eggs (Drent et al. 2006). These pressures produce a race for optimal early arrival on the breeding grounds. Yet, synchronized arrival and breeding may be more important than early arrival per se in colonial species. Indeed, food supplementation successfully advanced laying date in 70 % (n = 46) of experiments involving solitary nesting species compared to only

27 % (n = 11) of experiments with colonial breeders (reviewed in Nager 2006). In Common Murres earlier breeding was favoured in general but deviation from mean laying date (either earlier or later) resulted in reduced success (Reed et al. 2009; Hatchwell 1991).

Arrival synchrony within individual pairs of colonial breeders is likely important. Individual gannet pairs form on the breeding grounds, and they may rely upon specific relative individual migratory schedules to synchronize their yearly reunion (Gunnarsson et al. 2004). Indeed, it may be that initial pairing of young breeders is mediated by similar individual migratory schedules that brought them to the colony at the same time in the first place (Gunnarsson et al. 2004). Gannets are aggressively territorial and defend their nest site throughout the breeding season (Nelson 2005). Theft of nest material, (sometimes bloody) fights between adults and attacks on neighbouring chicks are common. Therefore, synchronous arrival to claim and defend the nest site would seem to be of utmost importance in this and other seabirds (Catry et al. 2009; Phillips et al. 2006, 2005). Predation may be the largest source of mortality for some seabird species (Hatchwell 1991) and synchronous arrival and breeding provides predation dilution through predator swamping (Reed et al. 2006; Hatchwell 1991). Although overall predation rates of adult and young gannets are small (Mowbray 2002), gulls (*Larus* spp.), Bald Eagles (*Haliaeetus leucocephalus*) and foxes (*Vulpes* spp.) do occur (in at least some years) at all gannet colonies in this study.

Effect of winter destination. Winter destination affected colony departure date. Gannets traveling to the northeast zone departed later than those destined for the

southeast zone but no difference was detected in the departures for other zones. Northeast-bound birds also had the greatest variation including the earliest and latest recorded departure dates (Figure 19). Similar to gannets, Streaked Shearwaters (*Calonectris leucomelas*) also displayed differences in departure date depending on destination (Yamamoto et al. 2010). Shearwaters taking a coastal route from the breeding colony in Japan to the closest wintering area in the South China Sea departed later and took longer to reach their destination than those crossing the open west central Pacific to winter off northern New Guinea and in the Arafura Sea. Yamamoto et al. (2010) hypothesized that this difference was due to the productivity of the waters encountered on the different routes; birds going further crossed less productive waters and therefore crossed quickly. The routes to all gannet winter zones overlapped, but there may have been differences in the quality of each winter area. With the northeast zone's close proximity and very productive hotspots for wintering, perhaps the timing of departure is not as critical as for the southeast.

Colony arrival date did not differ for migrations initiated from the different wintering zones. Instead, birds wintering in more distant areas departed earlier in order to arrive at the colony with relative synchrony. The range in departure dates from the earliest start date in the Gulf of Mexico to the latest departure from the Gulf of Maine was 62 days or about four days per degree latitude. Birds have endogenous control cycles for moult, gonad development, and migration (Newton 2008; Gwinner 1986) and these rhythms interact with photoperiod to control migration timing. Subsequently, secondary environmental factors such as weather and food supply allow fine tuning of migratory

timing, potentially en route (Newton 2008). For birds that winter in a single hemisphere and away from the equator, latitude is encoded in photoperiod allowing birds from the same breeding populations to synchronize their arrival. Arrival timing of gannets breeding at Bass Rock showed little variation for birds returning from different sections of the eastern Atlantic and Mediterranean (Kubetzki et al. 2009). Arrival timing of Streaked Shearwaters (Yamamoto et al. 2010), Black-browed Albatrosses (Phillips et al. 2005), and Black-tailed Godwits (Gunnarsson et al. 2006) also did not differ by distance to wintering grounds. But, not all colonial breeding seabirds arrive in synchrony. Great Cormorants wintering close (< 300 km) to the breeding colony in Denmark returned 2-3 weeks earlier than those further away (Bregnballe et al. 2006). But, for cormorants wintering 301 – 2500 km away, arrival date was only weakly related to distance from the colony, which the authors hypothesize is due to more distant birds initiating migration earlier and joining up with intermediate-distance birds en route. The spring return route of gannets migrating from the most distant wintering areas in North America takes them through the nearer wintering zones where they almost certainly join (or perhaps trigger) local birds in migration.

Effect of colony and year. Colony and year influenced departure and arrival timing. Bonaventure Island birds departed earlier in the fall of 2005 than they had the previous year, and they returned to the colony later the following spring (2006) than did Funk Island birds that year. Further, in 2007, Funk Island birds returned to the colony even earlier again. Gannets are synchronous breeders and departure date is constrained by chick fledging (up to a certain limit). Chick growth and development are affected by a

variety of factors including environmental conditions and food availability which may be linked to colony arrival in spring, which itself may be affected by conditions during the previous winter and during spring migration (Sorensen et al. 2009; Norris 2005). Therefore, it is not surprising that local conditions could dictate colony-specific and year-specific departure timing.

Local spring conditions around the colony may also determine the precise timing of arrival. European colonies cover a broad range of latitudes, and there is a latitudinal gradient in the arrival date for these sites due to the temporal progression of hospitable conditions during spring (Wanless et al. 2008). Arrival dates at UK colonies at higher latitudes than Newfoundland are also much earlier, emphasizing the role of oceanography. Funk Island birds arrived almost two weeks later in 2006 than in the previous year although there was no detectable difference between 2004 and 2005 at Bonaventure Island. Funk Island is the most northerly and oceanic colony in North America, located in a area that is surrounded by winter pack ice in most years. The colony at Bonaventure Island is located on high cliffs whereas Funk Island is a low lying granite slab that can be over-washed by late winter storms. Local weather conditions in mid-April may be more variable and the effect of the NAO on arrival and breeding timing (Gaston et al. 2009; Hüppop and Hüppop 2003) more intense at this oceanic colony. Temperature can also affect arrival date in birds (Gunnarsson et al. 2006) and April temperatures at Funk Island may be more variable than the more temperate conditions at Bonaventure Island.

Effect of sexes. Females departed the colony five days earlier on average than males. This could be an adaptation to equalize energy expenditure, since females feed chicks more than males late in the breeding season (Montevecchi and Porter 1980). Streaked Shearwater females fed chicks more frequently than males and also departed the colony five days earlier, ostensibly to satisfy a greater need to recover body condition before migration (Yamamoto et al. 2010). Despite the fact that female Black-browed Albatrosses provisioned chicks less, they still departed earlier than males, perhaps because the larger males were more capable of provisioning chicks and the females' early departure reflects equalization of investment relative to body size (Phillips et al. 2005).

Alternatively, the male gannets later departure may be socially mediated. Male gannets defend territories against potential usurpers throughout the breeding season (Nelson 2002) and perhaps their attendance at the nest site after female departure assists in establishing continued site ownership that may carry over into the next breeding season (Drent et al. 2003; Nelson 2002). Manx Shearwaters (*Puffinus puffinus*) showed no detectable difference in departure dates between males and females (Guilford et al. 2009) however, departure was defined as the exit from a 500 km buffer surrounding the colony. It is possible that this definition masked actual sexually-divergent colony departure, which was followed by a period of residency within the 500 km buffer (similar to Streaked Shearwaters; Yamamoto et al. 2010) before departing the buffer zone in synchrony. Many gannets also remained in the colony area before departing on migration and when colony departure was defined as the exit from a 300 km colony buffer, no sex-based difference in departure date was detectable.

Contrary to prediction, males and females did not differ in date of return to the colony in the population as a whole, although the male of the only tracked pair did arrive three days before the female. In gannets, pair formation and reunion occurs at the colony after the male (re-)establishes a territory (Mowbray 2002), and it is believed that males arrive earlier at the colony in order to do so (Nelson 2005). Male Australasian Gannet arrival preceded that of females (Ismar et al. 2010b) and Black-browed Albatross males also arrived 4 - 5 days earlier than females, a result that was attributed to their greater role in nest acquisition and defence (Phillips et al. 2005). But, earlier male arrival at the colony might not be a prerequisite for male-biased territory establishment and reclamation. Female gannets could arrive at the same time or even first, and then wait in the vicinity of the colony, checking back occasionally, until the territory is established. Sexes arrive synchronously in both Manx (Guilford et al. 2009) and Streaked Shearwaters (Yamamoto et al. 2010), but these species subsequently depart for a pre-laying exodus. It may be that the arrival timing of individual pairs was more finely tuned than in the population as a whole, with males of each pair arriving before females. Black-tailed Godwits retain mates by arriving within *ca.* 3 days of one another (Gunnarsson et al. 2004) which could be the result of strong individual migration schedules that caused these birds to arrive in synchrony and pair in the first place (Battley 2006). Examination of the arrival time data for gannets showed that many birds stayed for a short period (less than one day) on their first visit to the colony and departed for a variable number of days before arriving again, their attendance becoming more regular as time passed. For females, these visits could correspond to checking to see if their partner has established

the territory. An analysis of the timing, number and length of early-season colony visits by males and females might shed more light. Better still, tracking of both members of mated pairs over several breeding seasons would address this question.

4.2.2 Distance, duration and speed of migration

Migratory distance and duration showed considerable individual variability even within birds destined for the same wintering zone (Figure 18 and Figure 19). The overall distance covered between colony departure and arrival on the winter grounds varied by an order of magnitude (1,304 – 13,584) and duration by almost a factor of five (12 – 110 days). The greatest variation in distance and duration occurred in migrations to the northeast sector. This was driven largely by the fact that some (but not all) of these birds had extensive stopovers immediately following colony departure or upon reaching the American coast at Cape Cod, where small daily distances during many days of circuitous travel accrued to large total distances.

One gannet also undertook a visit to the Labrador Shelf early in migration and although gannets are not abundant in this area, they are known to occur on the shelf and in the Labrador Sea (Fifield et al. 2009). Direct-route migration distances of gannets breeding at Bass Rock (343 – 4654 km; Kubetzki et al. 2009) were similar to those for North American birds (*ca.* 1,000 – 4,000 km). The primary difference was that some Bass Rock gannets remained in the North Sea very close to the colony during winter which is not tenable for North American gannets due to weather and ice conditions.

The speed of migration was highly variable between individuals (mean: 136 km d^{-1}, range: 71 – 486 km d^{-1}) and was in the mid to high theoretical range for birds of this

size (Hedenström and Alerstam 1998). Surprisingly, male spring migration speed was slower than for females (although this difference was not significant), in contrast to the expectation that males would migrate faster to arrive earlier at the colony. Fall migration speed did not depend upon departure date, suggesting that the timing of arrival on the winter grounds was not critical and that there was no penalty for departing late from the colony.

Despite individual variation, winter destination had a significant effect on speed in fall but not in spring. In fall, migration speed was significantly faster to the more distant regions (southeast and Gulf of Mexico) than to the northeast. This was due to the effect of long stopover periods for many northeast-bound birds, resulting in lower overall speeds rather than a difference in daily travel speed per se. In spring migration speeds from each zone were more similar, although the fastest speeds were recorded by birds from the northeast. All (except one) of the 12 highest spring migration speeds were achieved by birds from the northeast zone. These migrations were relatively short (in distance and time) possibly indicating that such high speeds could not be maintained for long periods, likely due to the high cost of flight in gannets (Hedenström and Alerstam 1998; Birt-Friesen et al. 1989).

Migration speed for North American gannets (median: 120 km d^{-1}) was slower than that (250 – 450 km d^{-1}) for gannets breeding at Bass Rock (Kubetzki et al. 2009). This is likely due to the difference in how speeds were calculated. The speeds reported in Kubetzki et al. (2009) (for birds migrating to the most distant, African coast, wintering area) were based on the portion of the migration with the highest rate of change in

latitude (i.e. the steepest-sloped portions of the lines in Figure 15). They do not include stopover days spent near the colony (immediately after departure) or along the African coast before entering the (kernel-defined) winter area (Kubetzki et al. 2009). When only travel days (i.e. non-stopovers) are considered, the migration speeds of North American gannets are similar to those for Bass Rock gannets. Australasian Gannets that migrated from New Zealand to Australia exhibited similar speeds ranging from 125 – 350 km d^{-1} while covering about 2,300 – 5,000 km on migration (Ismar et al. 2011). Much of their journey was over open ocean, where speeds for North American gannets were in the range of 287 – 762 km d^{-1} (see section 4.3).

Gannet migration speeds and distances were slower and shorter than those for most other long distance migrating seabirds that have been tracked to date. Black-browed Albatrosses covered roughly 5,000 km from South Georgia Island to the Benguela Current in 3 to 6 days at speeds of about 800 – 1,770 km d^{-1}. Gray-headed Albatrosses can reach speeds of 750 – 950 km d^{-1} (Croxall et al. 2005) while female White-chinned Petrels covered 4,850 – 8,560 km at 310 – 610 km d^{-1} during their pre-lay exodus (Phillips et al. 2006). Sooty Shearwaters (*Puffinus griseus*) migrating in the Pacific Ocean used prevailing winds to cover 536 – 910 km d^{-1} (Shaffer et al. 2006) while Arctic Terns in the Atlantic Ocean covered 20,070 – 27,790 km at speeds of 390 – 670 km d^{-1} (Egevang et al. 2010). In contrast to gannets, these studies involved birds crossing large ocean basins with, in many cases, the assistance of wind. Further, all these species (excluding the tern) are procellariiforms which use less costly gliding flight and thus can

be expected to have higher flight speeds and migration distances than gannets (Hedenström and Alerstam 1998).

Migration speeds of North American gannets ascertained using geolocators were much higher than those reported in banding studies (Gaston et al. 2008). A similar result was found for gannets breeding at Bass Rock (Kubetzki et al. 2009; Wernham 2002). The determination of speed of migration from banding records is complex and fraught with assumptions (Wernham 2002) and therefore this disparity should not be overly surprising. Published speeds of migration based on banding data should be treated with caution and updated by tracking studies whenever possible.

4.2.3 Stopovers

All birds used stopover days during fall and spring migrations. This suggests that breaking the migration into periods of directed travel punctuated by more stationary periods is important for gannets. Yet, there was large variation in the number of stopover days used, and seven birds had only 0.5 stopover days in spring. There were no detectable differences in the number of stopover days used between sexes, colonies or years. Contrary to prediction, gannet stopover locations were not distributed randomly but instead were aggregated at several hotspots. Several of these highly productive hotspots coincided with areas of intense over-winter usage particularly in the Gulf of Maine, from Long Island to Chesapeake Bay and to a lesser extent along the coasts of South Carolina and Georgia. Although vacated during winter, a small area on the eastern Scotian Shelf in the vicinity of Sable Island and The Gully (the largest marine canyon in eastern North America) was used extensively in fall and to a lesser extent in spring. This region at the

edge of the continental shelf is highly productive due to physical forcing resulting in upwelling of nutrients. The Gully is a nationally and globally recognized area containing a rich diversity of species and habitats and is a Marine Protected Area. Several gannets had extensive stopovers in off-shelf oceanic regions east and south of the Grand Bank (more so in fall than in spring) as did and many satellite-tracked juvenile gannets (Montevecchi, Burke, Robertson, Hedd, unpubl data) suggesting that this deep-water region is a productive and important part of the gannet migration cycle for both age groups. Intriguingly, during spring migration, the temperature data indicated that several gannets spent one or more nights on land in the vicinity of Sable Island, suggesting that they roosted on this island or, less likely, on one of the nearby natural gas production platforms some of which are relatively small and unmanned. Such terrestrial (or industrial platform) roosting has not previously been reported for migrating gannets.

The number of stopover days varied by wintering area, although for fall, not in the manner expected. It was predicted that more stopover days would be required to reach more distant wintering areas. However, the number of stopover days during fall migration for birds targeting the Gulf of Mexico was not significantly different than that for gannets wintering in the northeast zone and migrations to both zones had significantly more stopover days than migrations to the southeast zone. However, there was no detectable difference in number of stopover days per day of migration between the winter zones suggesting that there was no difference in the daily cost of migration to each area. Instead, the difference in the number of stopover days was due to the difference in the duration (and speed) of migration to each zone.

While stopover days appear to be important and increase with distance traveled, there was extensive individual variability. Variability was greatest for birds en route to the Gulf of Mexico (followed closely by migrations to the northeast zone), with these birds having both the lowest and highest number of stopover days (Figure 18). For example, one bird from Funk Island made an essentially continuous migration to the Gulf of Mexico involving only two stopover days. Several birds had protracted periods of stopover, immediately after leaving the colony, in the Gulf of St. Lawrence and Laurentian Channel and on the southern Grand Bank and Scotian Shelf, lasting well into December. Many birds wintering in the northeast zone versus the other two zones differed in the way stopover days were used. Birds traveling to the other zones typically had periods of direct migration punctuated by stopovers at several locations including the Scotian Shelf, Chesapeake Bay, and the coasts of North Carolina/Georgia. While some birds traveling to the northeast zone had similar patterns, many did not. Many birds traveling to the northeast zone initiated essentially direct migrations (with or without stopovers on the Scotian Shelf) across the eastern Gulf of Maine to intersect the American coast around Cape Cod. These birds subsequently drifted slowly with much circuitous routing (i.e. most days classified as stopover) southwards towards their winter home range areas. Therefore many of the "stopover" days for northern zone migrants were really part of a slow drift more akin to dispersal than true migration. Although there was considerable individual variability, these observations, along with the fact that migrations to the Gulf of Mexico were faster indicate that, in general, migration timing to the northeast zone was less critical than to the southeast or the Gulf of Mexico.

Very few seabird tracking studies have addressed stopover/staging areas directly. Some Bass Rock gannets moved to the North Sea and Norwegian Sea for a few days to a few weeks before continuing their fall migration and this behaviour did not differ by winter destination (Kubetzki et al. 2009). Likewise, in spring most birds migrated to areas north of the colony before returning to breed (Kubetzki et al. 2009). All Manx Shearwaters tracked from the UK to South America made stopovers involving both sexes with roughly equal frequency between the outgoing and return migrations (Guilford et al. 2009). These stopovers were associated with behaviour that was similar to foraging, and Guilford et. al (2009) concluded that they likely serve the same refuelling function as they do in landbirds. Curiously, other shearwater species including Sooty (Shaffer et al. 2006) and Streaked (Yamamoto et al. 2010) have not displayed stopover behaviour during long-distance migration. Yet, Cory's Shearwater (Dias et al. 2010) and other seabird species as diverse as Black-browed Albatross (Phillips et al. 2005), Arctic Tern (Egevang et al. 2010) and Little Gull (Bellerby et al. 2000) have. This implies that the use of stopovers is a flexible trait between (and perhaps within) seabird species and much remains to be discovered regarding the reasons underlying these differences.

4.2.4 Consistency of timing and stopover site fidelity

Several aspects of timing and movement were highly consistent for repeat migrations. There was no detectable difference in the values of all parameters between years (all paired t-tests non-significant). This suggests a lack of wholesale shifts in the timing of migration and use of stopovers between years. Repeatability was significantly high for some, but not all parameters. In fall, migration duration, distance and arrival date

on the winter grounds showed significant repeatability within individuals across years, as did the departure date from the wintering area and the duration and distance of spring migration. Given that gannets displayed strong winter site fidelity, it is not surprising that the duration and distance of fall migration were more consistent within individuals than between them. Yet, gannets were individually consistent in the date of arrival on the winter grounds even though their departure from the colony was not. This suggests that gannets have individual programs for the duration and distance of migration and for the timing of arrival on the winter grounds. Likewise the repeatability of spring departure date supports the idea that gannets have an endogenous seasonal rhythm that is likely triggered by photoperiod. The significant repeatability of these parameters implies that they have a strong genetic component. In contrast, the initiation date, number of stopover days and speed of fall migrations were not significantly repeatable nor were the number of stopover days, speed and date of arrival in spring. This implies that these factors have a greater environmental component that determines their timing and magnitude. The date of fall migration initiation is likely constrained by chick development (see discussion in section 4.2.1). The number of stopover days and speed of migration are likely strongly affected by conditions encountered during the migratory journey. Poor weather and strong head winds would decrease speed of migration and require more frequent stopovers to replenish energy reserves at sites where productivity and interference competition from conspecifics could combine to determine the length of stopover. The timing of arrival in spring may be affected by local conditions near the colony (Bregnballe et al. 2006; Frederiksen et al. 2004). It is therefore intriguing that consistency

in arrival timing was found for Bonaventure Island (but not for Funk Island) when colonies were considered separately. However, these results should be viewed cautiously since samples sizes were small (especially at Funk Island) and only two consecutive years were considered.

Only a relatively small number of studies have reported migration timing in seabirds and even fewer have tracked the same individuals more than once. Fewer still report on the full suite of migration timing parameters presented here. A variety of descriptive (Phillips et al. 2006) and statistical procedures have been used to assess inter-year consistency in migration timing, including correlation (Phillips et al. 2005), paired t-test and repeatability (Dias et al. 2010; Battley 2006; Catry et al. 1999). Although these all measure consistency in some way, there are subtle differences between them, making comparisons between studies potentially problematic. For example, paired-t-tests determine whether, in the population as a whole, the mean of the individual differences between two measurements of a migration timing variable is significantly different than zero. But this is not the same as repeatability which measures whether an animal is more (or less) variable in its behaviour than the variability in that behaviour in the population as a whole. Example datasets can easily be constructed that show inconsistent timing via paired t-tests (i.e. a shift in mean response) but are still highly repeatable, displaying similar relative variation for each individual. Attention must therefore be paid to how consistency is measured when comparing studies.

Phillips et al. (2005) report remarkable inter-year consistency in migration timing parameters for Black-browed Albatrosses, except for the date of colony departure which,

as in gannets, was determined by breeding status and failure date. They found significant correlations in date of winter area departure, duration of migration, and arrival near the colony, but no consistency in use of staging (i.e. stopover) areas and concluded that consistency in migration timing may imply a major genetic component of control in individuals. They go on to hypothesize that albatrosses must have an endogenous timer (Gwinner 1986) that is cued by environmental factors such as photoperiod. Dias et al. (2010) tracked Cory's Shearwaters to the same (or different) winter locations in multiple years and found consistency (repeatability > 0.51) in the timing of departure and arrival from both nesting and wintering areas, but also failed to find consistency in the use of stopover sites. Bar-tailed Godwits (*Limosa laponica*) also displayed strong repeatability ($r = 0.83$) in adult departure date from the wintering area (Battley 2006). Repeatability of departure date in immatures was somewhat less ($r = 0.77$), implying optimal departure date was refined with age. Two further studies on passerines have shown significant repeatability ($r = 0.39$) for fall departure date in Blackcaps (*Sylvia atricapilla*; Pulido et al. 2001) and spring arrival in Barn Swallows (*Hirundo rustica*; r = 0.51; Moller 2001). These results are consistent with those for gannets, with the exception that gannets did not display overall repeatability in colony return dates. This difference between passerines and shorebirds, and gannets is not surprising given the differing selective pressures affecting each group (Reed et al. 2009; Drent et al. 2006; Hatchwell 1991). The consistency in arrival date for Black-browed Albatrosses (Phillips et al. 2005) and the repeatability of Cory's Shearwater arrival dates (Guilford et al. 2009) were both for individuals from the same colony. When gannet colonies were considered separately,

Bonaventure Island birds displayed repeatability in colony arrival date, but Funk Island birds did not. But, sample size was quite limited at Funk Island (n = 6) and conclusions thus difficult to draw. Procellariiforms have a mating system that involves a pre-laying exodus and the effect of this difference on relative arrival repeatability is unknown. Finally, a caveat about repeatability: although repeatability is often interpreted as an upper limit on heritability (Falconer 1981), this study and most of the others referenced above were conducted in only two or three successive years. Yet, repeatability over more than two years can decline rapidly. Catry et al. (1999) showed that both simulated and measured repeatability of laying date in Great Skuas (*Stercorarius skua*) declined to almost 0 when a lag as small as five years was considered. They hypothesized that both age-related effects and environmentally-induced changes in the ranking of plastic phenotypes may be responsible for this phenomenon and conclude that "most traits of interest cannot be permanent in a variable environment". Continued and repeated long-term tracking of gannet migrations will address the extent of consistency in their consistency.

4.2.5 Fall versus spring migration

In comparison to fall, spring migrations were shorter in time and distance and executed with an average of 1.5 times greater speed using fewer stopover days. Similarly, Gaston et al. (2008) report spring speeds of 2 – 4 times faster than in fall using band returns. In fall, birds are freed from the constraints of central place foraging and have many months before they are due back at the colony again and may not be under pressure to migrate at maximum speed (Newton 2008). With several highly productive stopover

areas to choose from along the route, the timing of fall movement is less constrained in comparison to spring (McNamara et al. 1998). This also implies that the timing of arrival on the winter grounds is not critical suggesting relatively predictable food supplies in wintering areas. In spring, gannets have somewhere important to go and are in a hurry to get there. At this time, they are constrained to arrive early enough, and in synchrony, at the colony to secure their territories and commence breeding in the relatively brief summer season. Since their arrival typically precedes that of abundant prey and good weather days (Nelson 2002), the increase in migration speed with departure date (contra that for passerines; Newton 2008) suggests that birds wait as long as possible on productive winter or stopover areas to maximize energy intake.

Gannets used fewer stopover days during spring migration (seven birds had only 0.5 stopover days) further confirming the urgency of spring migration. Nonetheless, the number of stopover days per day of migration was similar to fall, indicating physiological constraints on the rate of migration imposed by the rate of energy intake (Weber et al. 1998; Hedenström and Alerstam 1998). In contrast, Northern Gannets breeding at Bass Rock had spring migrations that were about as long as fall, however no detailed analysis of timing has been conducted for these birds (Kubetzki et al. 2009). In contrast, two of three Australasian Gannets had more protracted and spatially variable pre-breeding (spring) as opposed to post-breeding (fall) migrations (Ismar et al. 2011). Although, Black-browed Albatrosses that left their wintering area late traveled more slowly and at higher latitudes than earlier birds, they compensated by using fewer stopovers (Phillips et al. 2005). In one study of Cory's Shearwater (González-Solís et al. 2007), spring

migration duration (23 ± 7 d) were slightly longer than fall migrations (19 ± 10 d; although the ranges overlapped completely), while in another study (Dias et al. 2010) spring migration (about "three weeks") was shorter than fall (36 days; no SD or ranges provided). In contrast, spring migrations were significantly longer than fall for male Manx Shearwaters and slightly shorter for females (Guilford et al. 2009). But, the routes of fall and spring migration different in the studies involving procellariiforms making comparisons of timing with gannets problematic. Further detailed analysis of the spring and fall migration timing in gannets (particularly in Europe) and in their congeners and other seabirds in general will shed more light on these patterns.

4.3 Trans-Atlantic migration

Northern Gannets breed throughout the North Atlantic Ocean and questions about the species' geographic radiations, large-scale population interactions and connectivity are unresolved. This study is the first to describe a normally continental shelf/slope migrant seabird with two such divergent migration strategies, and one of a very few involving such differing strategy rates for two populations that breed in relative proximity: the Bonaventure Island population remaining entirely in domestic waters, and the Newfoundland population employing a dual strategy. The discovery of a connection in a seabird between the two major world breeding divisions (North American and European) of a seabird separated by the Atlantic Ocean basin that was previously considered a migratory divide (Nelson 2002) is novel.

During winter, some seabirds range widely (Shaffer et al. 2006; Croxall et al. 2005; Weimerskirch and Wilson 2000), and some occasionally stray, particularly immature birds. Nine banded Northern Gannets were documented to cross the Atlantic Ocean in this study and the details for only six of these were previously published (Gaston et al. 2008). Trans-oceanic band recoveries have been almost exclusively from Newfoundland gannets, mostly immature birds. The one-off nature of band returns made it impossible to determine whether trans-Atlantic banded gannets were undertaking intentional migrations, but these were considered likely to be accidental, one-way crossings at best (Gaston et al. 2008; Nelson 2002). Thus, the discovery of trans-Atlantic round-trip migration and wintering off the coast of Africa by three geolocator-equipped birds, one from each of three Newfoundland colonies was surprising. Trans-Atlantic migrations involved birds in 2005-06 from colonies separated by 350 km, a repetition of the same route in 2006-07 by one of these birds (the only one tracked subsequently) and a gannet from the third colony that lies between them in 2009-10. These tracks indicate that trans-Atlantic migration is a deliberate tactic, not an accidental event. Instead, although sample size is small, it implies the likely regular use of a radically different migratory tactic by a small segment of the population.

Trans-Atlantic migration involved the rapid crossing of *ca.* 4,000 km of open ocean at speeds exceeding those normally found in continental shelf migrations. Long distance migrants often "wait" for favourable conditions to enhance flight performance (Murray et al. 2003; Alerstam et al. 1993). Some of the trans-Atlantic migrants experienced unfavourable headwinds on days leading up to their departures from North

American waters but then exploited ocean-basin weather systems to complete astonishingly rapid (and in some cases remarkably synchronous) and direct flights across the North Atlantic Ocean in only five days. The timing of departures in relation to the movement of favourable weather systems suggests decision-making on the part of trans-Atlantic migrants. These ocean-crossing gannets are also more likely to depend on "finer tuned" temporal migratory initiations than conspecifics moving along continental shelf edges, and many long-distance migrant seabirds (Sooty Shearwaters; Cory's Shearwaters; Gray-headed Albatrosses and Wandering Albatrosses) exhibit highly synchronized large-scale weather-induced movements (Shaffer et al. 2006; Catry et al. 2004c; Murray et al. 2003; Spruzen and Woehler 2002). East-to-west return migrations were temporally and spatially variable; in 2006 and 2010 two gannets re-crossed the Atlantic in 4 – 5 days, the other met unfavourable winds and took 15 days in 2006 and 16 days in 2007.

Consistent long-term oceanic wind patterns shape the evolution of migratory and foraging activities in seabirds (González-Solís et al. 2007; Shaffer et al. 2006; Grémillet et al. 2004; Murray et al. 2003; Weimerskirch et al. 2002; Berthold 2001). The regular eastward movement of weather systems across the North Atlantic provides a predictable series of "weather bridges" that assist gannets in rapid west-to-east traverses across open ocean. By selectively positioning themselves with respect to wind patterns associated with these systems, seabirds can also exploit them (perhaps less effectively) for east-to-west traverses. Because movements of these weather systems across the North Atlantic are facilitated by the same large-scale climate systems (i.e. Icelandic Low and Azores High Pressure Systems) that drive the North Atlantic Oscillation, climate change can be

anticipated to influence the migratory behaviour of these oceanic migrants (Weimerskirch et al. 2002).

The Northern Gannets' two congeners are also capable of long distance, trans-oceanic movements. Both adult and immature Australasian Gannets disperse across the Tasman Sea to winter on the east coast of Australia (Ismar et al. 2011; Ismar et al. 2010a), a distance of *ca.* 2,500 km. One Australasian Gannet crossed the Indian Ocean and settled in an African Cape Gannet colony (Dyer 1995), while another ventured to Brazil (Nelson 2005). Likewise, a Cape Gannet mated with an Australasian Gannet at a colony in Australia (Nelson 2005), and an adult accounted for the first Pacific Ocean record in Peru (Garcìa-Godos 2002). Thus, although trans-oceanic journeys are rare for adult gannets, it is clear that the capability to do so is well represented in this genus.

Colony departure dates of trans-Atlantic migrants were similar to those for other birds from the same colony (or region) in the same year, further emphasizing that this parameter does not depend upon winter destination, but is instead determined by conditions at the colony. Spring departure dates from the coast of Africa were similar to departure dates for North American gannets but were later than those for Bass Rock gannets wintering in the same area (Kubetzki et al. 2009). Colony arrival dates for 3 of 4 trans-Atlantic migrants fell within the range of their domestic conspecifics for a given colony and year. This suggests that trans-Atlantic migrants are under the same selective pressures for synchronous arrival at the colony, rather than synchronous departure from the wintering area. However, contrary to the other trans-Atlantic migrants, the female bird F's arrival at the breeding colony in spring was not synchronized with other Funk

Island birds tracked during the same year. Bird F had the earliest winter area departure date of any bird in 2006 and the second earliest in 2007 and arrived at the breeding colony 3 – 4 weeks in advance of any other tracked bird in both years. The consistency of this gannet's routing and early arrival and the fact that its date of African coast departure was more similar to the departure dates of Bass Rock gannets, hints at a close genetic linkage between some trans-Atlantic North American migrants and European gannets.

Trans-Atlantic migrants also exhibited much higher average flight speeds (287 – 762 km d^{-1}) than their domestic counter-parts (71 – 486 km d^{-1}). Gannet positions were smoothed using a 2.5 day sliding window filter that diluted the large daily displacements during trans-Atlantic portions of the migration, particularly at the start and end of crossing, with the smaller displacements over continental shelves. An examination of daily longitudinal shifts of unsmoothed positions during crossing revealed that wind-assisted gannets may have actually reached speeds of up to *ca.* 1200 km d^{-1}. These speeds rival or exceed those of Gray-headed Albatrosses (750 – 950 km d^{-1}), White-chinned Petrels (310 – 610 km d^{-1}), Sooty Shearwaters (536 – 910 km d^{-1}), Arctic Terns (390 – 670 km d^{-1}) and Bar-tailed Godwits (800 – 900 km d^{-1}) crossing large ocean basins (Egevang et al. 2010; Gill et al. 2009; Shaffer et al. 2006; Phillips et al. 2006; Croxall et al. 2005).

The trans-Atlantic strategy carries different risks and benefits compared to domestic wintering. Normally coastal shelf migrants, gannets are presumably constrained by poor food availability in the deep central ocean, making ocean-crossing risky and necessitating precise and rapid execution. Streaked Shearwaters migrated faster over the

low-productivity south central Pacific en route to seas off northern New Guinea than did birds from the same colony migrating over relatively productive coastal waters to the South China Sea (Yamamoto et al. 2010). However, recent tracking studies of Arctic Terns (Egevang et al. 2010), Cory's Shearwaters (Magalhães et al. 2008), Great Skuas (Sittler et al. 2011) and murres (*Uria* spp.) (L. McFarlane-Tranquila unpubl. data) indicate stopovers for considerable periods near the Mid-Atlantic Ridge where prey is presumably more abundant due to upwelling. One gannet from the present study spent *ca.* 5 days in this area on its return journey from Africa (Figure 23) and one satellite-tracked juvenile spent weeks in the mid-Atlantic before returning to the North American coastal shelf (Montevecchi, Burke, Robertson, Hedd unpubl data). Likewise, a Northern Fulmar (*Fulmaris glacialis*) likely crossed the North Atlantic several times in a single non-breeding season (Mallory et al. 2008).

The wintering area of the gannets which made trans-Atlantic crossings from Newfoundland overlapped both spatially and temporally with that of gannets from eastern Atlantic colonies (Kubetzki et al. 2009; Nelson 2002; Wanless 2002) and other seabirds (González-Solís et al. 2007; Furness et al. 2006). The 75 % kernel winter ranges of gannets from Bass Rock, Scotland (Kubetzki et al. 2009) were intermediate in size between the core (50 %) and home (95 %) ranges of the birds in this study, indicating a similar pattern of space use. This part of the Canary Current system is extremely productive and its upwelling has been characterized as the "most intense and persistent in the western Palearctic" (Wynn and Knefelkamp 2004). Such a migration strategy could be maintained by the benefits of wintering in this region, especially since gannets and

other seabirds scavenge discards from fisheries that target key avian prey (sardines *Sardinella* spp., pilchards *Sardina pilchardus*; Camphuysen and van der Meer 2005).

Compared to the western Atlantic population, the eastern Atlantic has more than six times more colonies and 3.5 times more gannets (Nelson 2005). These circumstances and the retreat of the North American Wisconsin glaciation about 10,000 years ago suggest that gannet colonies radiated from east to west, similar to other North Atlantic seabirds (e.g. Manx Shearwater; Robertson 2002; Black-headed Gull, *Larus ridibundus*; Montevecchi et al. 1987). In this regard, it is paradoxical that trans-Atlantic movement has never been recorded in eastern Atlantic gannets despite the fact that approximately 60,000 birds have been banded there, almost five times more than in North America (Table 14; Nelson 2002; Wanless 2002). A single gannet banded in Iceland was recovered in northwest Greenland (Peterson 1998 cited in Wanless 2002) and seven have been recovered in Europe (Wanless 2002). Further, none of the 22 geolocator-equipped adult gannets tracked from Scotland crossed the Atlantic (Kubetzki et al. 2009) although nine of these wintered in the same area off West Africa as the trans-Atlantic migrants from Newfoundland. Other species of birds that have colonized the New World through trans-Atlantic crossings (e.g. Northern Wheatear *Oenanthe oenanthe,* Common Ringed Plover *Charadrius hiaticula,* Red Knot *Calidris canutus islandica*) continue to retrace their ancestral routes of radiation during migration (Newton 2008; Sutherland 1998). The higher rate of Atlantic Ocean crossing by birds from Newfoundland colonies (versus Bonaventure Island) and the overlap in winter with European gannets could reflect a retained genetic predisposition for returning to coastal West Africa in winter. Such a

migratory behaviour could result from more recent or ongoing trans-Atlantic population exchanges between Newfoundland and the eastern Atlantic population. Alternatively, it may simply be that, due to geography, more Newfoundland juvenile gannets are carried across the Atlantic by storms whereupon they follow other gannets south to Africa. Presumably, these birds would subsequently return to their natal colonies to breed but maintain their initial migratory route to Africa in subsequent years. In this light, it is interesting that a juvenile gannet from Cape St. Mary's initially moved east with an intense low pressure system across the North Atlantic (reaching *ca.* 20° W in late October 2010) returning to North American waters only after the system had passed (Montevecchi, Burke, Robertson, Hedd, unpubl data). Further, it is intriguing that the only three known North American Great Black-backed Gulls (*Larus marinus*) to have undertaken trans-Atlantic migrations were hatched and banded in eastern Newfoundland, whereas no trans-Atlantic migration has been detected for birds breeding to the west of Newfoundland; and similar to gannets, no European-banded Great Black-backed Gull has been recovered in North America (Wille et al. 2011). This again underscores the need to understand how genetic and environmental factors interact to affect migration, and the need to investigate and compare migratory patterns between parents and offspring.

Two such divergent migratory programs rarely co-exist in a single population (Newton 2008). The occurrence of multiple migration strategies to such broadly disjoint winter areas within the same seabird populations (particularly from the same colony) has only rarely been reported. Black-browed Albatrosses breeding in South Georgia have three wintering areas, two of which are each used by only 3 % of the population (Phillips

et al. 2005). Most birds wintered in the Benguela Current system while one wintered in the southwest Atlantic and another off southeastern Australia. Based on breeding success and migration timing, the authors concluded that the more distant wintering areas were in no way sub-optimal and that choice of destination likely had a major genetic component. Gray-headed Albatrosses displayed three distinct migratory strategies, one of which involved global circumnavigation (Croxall et al. 2005). Cory's Shearwaters breeding at the Azores, the Canary Islands and in the Mediterranean showed colony-based preferences for one of three major wintering sites, two in Africa and one in South America but there was substantial mixing (González-Solís et al. 2007). More than half of the Cory's Shearwaters breeding at Selvagem Grande Island off the northwest coast of Africa wintered in the Benguela Current while the rest were distributed among five other wintering areas including the northwest Atlantic, and the Brazilian, South Central Atlantic, Canary and Agulhas currents (Dias et al. 2010). Streaked Shearwaters breeding in Japan wintered in three separate regions, although these were not as widely separated at the gannets' North American and African destinations (Yamamoto et al. 2010). Sooty Shearwaters breeding at two colonies in New Zealand followed similar migratory routes across the equator and overlapped completely in one of three distinct winter regions in the north Pacific (Shaffer et al. 2006). These examples all involve procellariiform species, and in contrast to gannets, regularly perform long-distance migration and foraging trips that cross ocean basins.

Gannets are not known to form pair bonds on the wintering grounds, so this migratory connection may not imply large-scale gene flow between eastern and western

Atlantic populations. Though because gannets, like shearwaters (González-Solís et al. 2007), migrate in groups, it is possible that inexperienced immature birds could follow more experienced conspecifics during return migration and begin breeding at colonies on the opposite side of the Atlantic Ocean from which they were hatched. In this light, the recovery of an adult Newfoundland-banded Northern Gannet in Iceland during the breeding season (Table 13) is consistent with cross-oceanic gene flow. Finally, the overlap between European and North American populations is important for disease epidemiology. There has been much concern over the global spread of Avian Influenza Virus within wild bird populations (Winker and Gibson 2010; Koehler et al. 2008; Munster et al. 2007), and the inter-continental overlap of Northern Gannets in winter could provide a possible vector for pathogenic transmission (Koehler et al. 2008; Olsen et al. 1995).

4.4 Ecological, evolutionary and conservation implications

The ecology and evolution of wintering strategies and the selective pressures that shape them, both proximally and ultimately, form a complex web of interaction. The degree of population structure/connectivity during winter is a direct result of (and an input into) this interplay. An important ecological advantage of weak connectivity/population structuring is that it allows more efficient exploitation of available food resources, when birds spread out over a broad winter range. Such a pattern also limits excessive competition (Salomonsen 1955) that could occur if all gannets wintered in the northeast zone as close to the colony as possible. This lack of strong

population structuring means that birds from any one breeding population experience a variety of areas and selective pressures during winter implying that, in evolutionary terms, any adaptive variation in different breeding populations must be due to selective pressures that act during the breeding season (e.g. Garthe et al. 2007b). The degree of gene flow among breeding populations will influence the extent to which such variation can develop. Gannets display strong natal philopatry and adults rarely switch colonies (Nelson 2002), so there appears to be little opportunity for gene flow; conditions that favour adaptive variation. This can cause severe population crashes if long-term foraging conditions within range of the colony deteriorate and birds lack the flexibility to move the colony to a better location (Pichegru et al. 2010). But, dispersal to non-natal colonies does occur occasionally, which works to counteract adaptive variation. Further, natal dispersal could have a complex relationship with migratory behaviour, depending upon the extent of genetic and environmental influences on the transmission of migratory traits across generations (Webster and Marra 2006). More research is needed to unravel the relative contributions of genetics and environment in determining migration and winter location.

Weak connectivity implies substantial genetic variation for wintering area and a lack of strong local adaptation to particular wintering sites (Webster and Marra 2006). Local adaptation may be advantageous when prey resources are predictable (Weimerskirch 2007) particularly during breeding when adult gannets are limited to central place foraging (Hamer et al. 2007). Strong local adaptation to winter areas might however be detrimental to survival in the face of dynamic and stochastic ocean

conditions. Thus, weak connectivity is associated with better adaptability to changes in winter conditions in the population as a whole (Webster et al. 2002). During breeding, Northern Gannets show considerable flexibility in foraging behaviour associated with variations in oceanographically driven prey fields (Garthe et al. 2011; Montevecchi et al. 2009; Hamer et al. 2007), so it is expected that they could also use such flexibility to their advantage over the more extensive spatial and temporal scale of migration and wintering. If conditions become unfavourable enough to affect survival in one part of the winter range, the population as a whole could suffer reduced losses if there is substantial behavioural flexibility and/or genetic variation for winter location (Berthold 1996).

Weak connectivity has positive and negative implications for gannet conservation. On the positive side, widespread mixing of populations across a large geographic area reduces the risk that any one threat will significantly affect a single breeding population or the species as a whole. Even if a non-localized threat such as climate change affects gannet winter survival in some regions, the gannets' broad winter latitudinal range could help to mitigate serious population level effects, presuming that the extent of change differs in different wintering regions. However, population overlap in winter results in broader geographical range of effect from such threats. The *Deepwater Horizon* explosion and blowout in the Gulf of Mexico during 2010 and mass die-offs in the southeast sector (and in Chesapeake Bay) carry over across seasons to affect distant and broadly separated breeding populations (Montevecchi et al. 2011). This complicates the assessment and response to such threats which often require monitoring and interaction with birds on the breeding grounds. The cost and logistical constraints involved in

carrying out this work at multiple colonies is thus magnified. Furthermore, such a year-round distribution across multiple national and state/provincial (and departmental) jurisdictions complicates the coordination of response, reserve network design (Norris et al. 2006) and planning for effective conservation. Even broad geographic distribution is no guarantee against some threats. The majority of gannets wintered in relative proximity to the outflow one or more large river systems (e.g. the Hudson and Mississippi Rivers, the Delaware Bay and Chesapeake Bay estuary systems), and these rivers are the source of considerable contaminants that could threaten gannets (Rattner and McGowan 2007). Thus, while gannets may display broad *geographical* distribution, they may have a narrow distribution on the "contaminant landscape", putting the entire North American population at risk.

The consistency and repeatability of migration timing implies that these are characteristics of individuals and under genetic control (Berthold 2001). If climate change alters the timing of prey availability at stopover sites or at the breeding grounds then a mismatch could occur between the timing of events in wintering and breeding areas, possibly resulting in sub-optimal arrival timing and reduced fitness (Both and Visser 2001). Climate change is likely to vary by latitude thereby affecting birds returning to colonies at different latitudes differently. Birds wintering far from the breeding grounds have evolved departure timing based on endogenous rhythms fine-tuned by environmental cues that allows them to arrive when environmental conditions are appropriate on the breeding grounds. But climate change may decouple this timing linkage causing a mismatch in timing of migration for more distant migrants. Further,

climate change may decouple the relationship between climate indices that birds also use to time their migration (Frederiksen et al. 2004) and the extent of this decoupling may vary by wintering area. Birds wintering closer to the breeding grounds have the opportunity to sample local environment conditions and arrive with more advantageous timing (Bregnballe et al. 2006).

The date of breeding has been getting later for gannets in the eastern Atlantic (Wanless et al. 2008) but no difference in timing was detected for North American gannets in this study. Even if the lay date for North American gannets was to become later, the gannets' current migration schedule would seem at first not to be problematic; they would still arrive in plenty of time to breed. But, if prey becomes unavailable early in spring due to timing effects of climate change (Walther et al. 2002), then birds arriving with current scheduling could pay a survival penalty (Drent et al. 2003). Moreover, if the spring peak in food availability were to become earlier (Gaston et al. 2009), gannets might be constrained to sub-optimal arrival by inflexible migration timing (Both and Visser 2001).

The ability of gannets to adapt to an altered environment will depend on the level of genetic variation or behavioural plasticity in timing (Pulido 2007). Artificial selection can quickly alter the timing of migration; Blackcaps breeding in Germany changed their timing by one week in just two generations (Pulido et al. 2001). This is good news; unless you're a gannet. The k-selected life history of gannets and other seabirds dictates that adaptation will be slow (Dias et al. 2010). Even if natural selection could act as quickly as observed in artificial selection experiments, gannets may not be able to respond

quickly enough due to their long generation time. The ability to respond plastically and the rate of response will depend on the extent to which migration timing and winter site choice are fixed (Catry et al. 1999). Flexibility in wintering site (Dias et al. 2010) and migration timing (Frederiksen et al. 2004) have been observed in other seabirds. The gannets' ability to evolve or adapt will determine the extent to which they are winners or losers in a changing environment (Hamer 2010).

5 Conclusion

This is the first study to track Northern Gannets electronically during winter in North America. Extensive banding efforts involving tens of thousands of individuals over several decades provided relatively little information on gannet winter strategies, whereas tracking a few tens of birds over several years has revolutionized our understanding. The wealth of information this technology has provided while causing minimal disturbance to a small number of animals is truly remarkable. The integration of banding and geolocator data provided a clearer understanding of the migratory strategies of gannets than either could provide on their own.

Gannets did not wander widely or randomly within their winter range, instead choosing to aggregate at hotspots that overlapped with the known distribution of prey. There was weak to moderate population structuring and most individuals remained in relatively small discrete winter areas. There was a dramatic and unexpected increase in winter usage of the Gulf of Mexico in comparison to historical banding data, likely shaped in part by changes in the relative abundance and distribution of prey. Both sexes

overlapped completely and range size was consistent on the winter grounds. Winter destination had the greatest effect on migration timing parameters and spring migration was faster than fall. Stopovers during migration likely served to replenish fuel reserves. Males departed the colony later than females in fall, but did not arrive at the colony first in spring.

The observed patterns of winter range size and distribution were consistent across years for both individuals and the population as a whole. Individual gannets displayed remarkable fidelity to wintering areas and stability in range size at global, continental and regional scales. Migration duration, route and timing of arrival and departure at these winter sites were also remarkably consistent.

This is the first study to report two strikingly different migration strategies (involving trans-Atlantic migration) in a continental-shelf migrant seabird. The significance of trans-Atlantic Ocean band returns (particularly adults) was reinterpreted in light of the discovery of round-trip trans-Atlantic migrations to Africa. The difference in the prevalence of the trans-Atlantic Ocean strategy among North American colonies was even more remarkable. Moreover, the absence of trans-oceanic recoveries of gannets from the eastern Atlantic contrasts sharply with those of North American gannets. The minor but unidirectional movement of gannets from the western to the eastern Atlantic Ocean in winter appears to reflect colony radiation in the opposite direction or alternatively a return to ancestral wintering grounds.

Although roughly two decades old, electronic tracking of seabirds is still in its infancy. The gannets in this study were tracked for a maximum of two years, leaving the

longer-term stability of individual wintering strategies unknown. Most tracking studies cover similar short time periods, lasting only one or two seasons/years. This pattern is representative of typical funding cycles and the length of graduate student programs. Few species and/or populations have been tracked to date. As technological devices become smaller and cheaper there is considerable pressure to focus on new (often smaller) species or novel populations of previously tracked species. But, longer term tracking will be required in order to address important threats such as climate change, which operate over extended time scales. This will require a concomitant increase in the perceived value of such "replicate" studies by both funding agencies and scientific journals. Repetition at this scale is a cornerstone of the scientific method that is too often ignored in the race to produce and publish the latest novel result. As tracking becomes more accessible and commonplace, it should be integrated and accepted as part of the regular and continuous monitoring of individuals and populations. Only in this way will tracking pay extended dividends to our understanding of the much neglected non-breeding period and allow us to address conservation concerns such as climate change. Continued (and continual) year-round tracking of adults and particularly their offspring, especially (for immatures) to eventual breeding colonies (Gillis et al. 2008) will permit significant progress to be made. This could be efficiently achieved by a combination of electronic devices and intrinsic markers including fatty acid signatures, stable isotopes and population genetic probes (Navarro et al. 2009; Gómez-Dias and González-Solís 2007; Furness et al. 2006).

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